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ARBOREAL ADAPTATIONS OF PEROMYSCUS, WITH SPECIAL REFERENCE TO USE OF THE TAIL*

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INTRODUCTION

ADAPTIVE modifications, be they morphological, physiological, or psychological, are of universal importance in the animal world. The literature of zoology contains abundant evidence that animals show marked adaptation for a variety of habitats. Despite the vast literature on adaptations, however, few measurements have been recorded of their actual effectiveness in nature or in the laboratory.

The ecologic diversity of the various forms of mice of the wide-ranging genus Peromyscus has long been recognized. Some peromyscus live in swampy areas, some in prairie lands, some in arid desert lands, and others in forested areas. Concomitant with ecologic diversity in habitat many forms exhibit structural characters which may be presumed to be adaptive. This is particularly noticeable in regard to pelage

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color, which in peromyscus and many other small mammals tends to be positively correlated with the color of the surface soil (Dice and Blossom, 1937: 106-8; Dice, 1940: 213-15). That this like coloration is really protective has been demonstrated by experiments (Dice, 1947).

With the exception of pelage color very little is known about the importance to peromyscus of characters which may be adaptive. Dice (1940: 215) suggested that the general correlation of tail length and hind-foot length with type of habitat may be essentially a correlation with habit; that is, the relatively longer tail and the relatively longer hind foot of the forest-dwelling forms, as compared with the prairie-dwelling, is possibly correlated with their semiarboreal habits. Since there has been too little information available to demonstrate such a positive correlation between body proportion and habit, the present study was largely designed to test this hypothesis.

The purpose of the investigation was threefold: (a) to study general arboreal performance in peromyscus, (b) to measure the arboreal behavior and ability of forms which in nature live in diverse types of habitat, and (c) to ascertain whether the long tail of a semiarboreal form is of greater aid to an arboreal life than is the short tail of forms which live in more open areas. The forms selected for study included five semiarboreal, four largely terrestrial, and one from a more or less intermediate habitat.

Although there are several references in the literature to climbing of peromyscus in nature, relevant experimental work in the genus is far more limited. Clark (1936) discovered certain consistent differences in geotropic behavior between very young mice of the semiarboreal and nonarboreal races he tested and Harris (1952) found that a terrestrial form and a semiarboreal form differed in their selection preferences for artificial habitats. The use of the tail as a balancing organ in house mice is described by Buck, Tolman, and Tolman (1925). Löhrl (1938) made laboratory observations of climbing ability in Apodemus, a genus of mice which appears to occupy some of the same ecologic niches in the Old World that members of Peromyscus do in the New. Apodemus sylvaticus, which reached its maximum density in a wooded-field habitat, was not, he found, demonstrably a less proficient climber than the generally longer-tailed, more exclusively forest-dwelling form A. flavicollis. A brief description of the use of the tail in climbing in Apodemus is also given by Löhrl (1938), based on the performance of captive mice trained to climb along small branches to obtain food. Dor (1937) studied the morphology of the caudal appendage as related to mammalian locomotion, and there are extensive works by Hatt (1932) and Howell (1932) which give an excellent survey of the use of the tail by ricochetal rodents. But all of this material, as well as that dealing with climbing in various nonperomyscan mammals, is related to the present problem in only a general way.

By reason of the paucity of specific information about climbing performance in peromyscus, the methods and apparatus used for testing in this study are largely original. It was necessary to devote much time to devising special techniques for measurement of climbing ability. The present report gives, therefore, only a partial survey of the scansorial adaptations within the genus.

Acknowledgments

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MATERIALS AND METHODS

Forms and Stocks

Five species, Peromyscus maniculatus, P. polionotus, P. leucopus, P. nasutus, and P. truei, are represented by the ten forms studied. A brief account of the collection of the original animals follows:

Peromyscus maniculatus bairdi (Prairie deermouse). -- Trapped by Merrel A. Taylor, in 1938, on the Todd Farm, near Fennville, Allegan County, Michigan.

Peromyscus maniculatus blandus (Chihuahua deermouse). -- Taken by W. Frank Blair, in 1938, near Tularosa, Otero County, New Mexico.

Peromyscus maniculatus gracilis (Forest deermouse). -- Trapped by W. Frank Blair, in 1940, at Pine Lake, Alger County, Michigan.

Peromyscus maniculatus nebrascensis (Sandhills deermouse). -- Trapped by Burton T. Ostenson and Palmer R. Sime, in 1935, near Kennedy, 40 miles south of Valentine, Cherry County, Nebraska.

Peromyscus maniculatus oreas (Cascades deermouse). -- Trapped by Lee R. Dice, in 1940, near Longmire, Mount Rainier National Park, Pierce County, Washington.

Peromyscus maniculatus rubidus (Redwood deermouse). -- Trapped by Lee R. Dice, in 1940, near Hood River, Hood River County, Oregon.

Peromyscus polionotus leucocephalus (Santa Rosa Island beach mouse). -- Trapped by W. Frank Blair, in 1942, on Santa Rosa Island, Santa Rosa County, Florida, opposite Camp Navarre, which is on the adjacent mainland.

Peromyscus leucopus noveboracensis (Wood mouse). -- Two stocks: one trapped by Ernest C. Driver, in 1943 and 1945, at Northampton, Hampshire County, Massachusetts; the other, by Lee R. Dice and B. Elizabeth Horner, in 1945, in Ann Arbor, Washtenaw County, Michigan.

Peromyscus nasutus nasutus (Juniper mouse). -- Taken by Lee R. Dice, in 1937, near Lincoln, Lincoln County, New Mexico.

Peromyscus truei truei (Pinyon mouse). -- Trapped by Lee R. Dice, in 1937, near Capitan, Lincoln County, New Mexico.

Inbreeding

Inbreeding of the stocks was kept at a minimum. Since all of them, however, except those of the form noveboracensis, had been in captivity for several years, a certain amount of inbreeding became imperative to maintain them. In spite of this, the body measurements of the mice used agree fairly well with those of the original animals of the several stocks. Although the animals available for study could not be expected to represent fully the respective wild populations, it is believed that they have provided reasonably valid measurements of the abilities and behavior characteristic of the natural populations.

Rearing and Handling

All recorded observations were made at the Laboratory of Vertebrate Biology of the University of Michigan, where the mice were maintained under essentially uniform conditions. The methods of rearing the mice varied only in minor details from those described by Dice (1929). The inverted aluminum nest pan, or "igloo" (Horner, 1947: 32), routinely placed in the cage of each mated female, was provided as a hiding place in many of the experiments.

Every effort was made to handle the mice gently and to accustom them to the presence of the observer. The cages were opened at frequent intervals and the nests cautiously examined. The mice were usually transferred from place to place, outside the cages, in glass water tumblers with the hand cupped over the open end. This method proved more satisfactory than the usual one of handling the mice with forceps, for it minimized the possibility of injuring their tails and produced less excitement in the captured animals. When it proved impracticable to induce a mouse to enter a tumbler, the animal was caught either in a live trap or in the cupped hands.

It was possible to tame the mice somewhat by conditioning them to a sound-food association. A sunflower seed was inserted through an opening in the wire mesh at the front of the cage and at the same time a squeaking sound was made. With few exceptions the mice quickly learned to respond to the auditory signal and readily took the seeds from the fingers. Sunflower seeds, highly prized by the mice, were never introduced into the food cup with the regular food supply, but were given only upon issue of the auditory signal or as rewards accompanying certain of the experiments.

In order to avoid foot injury a modification of the Laboratory method of individual identification, which utilizes toe cutting as well as ear punching (Dice, 1929: 122-23), was employed. For this study of climbing it was essential to limit the markings to ear punches. A system was devised employing both ears and only the ears. It ran up to 399 without duplication.

Body Measurements

In measuring the living, unanesthetized mice some modification of the usual method (Dice, 1932: 5-6) was required. Since measurements of live mice are likely to be less accurate than those of freshly killed animals, the body dimensions obtained are not strictly comparable with those obtained by the regular technique. The measurement of live, unanesthetized mice proved to be a two-person maneuver: the author made the measurements while another person held the mice. The modified procedure is given below.

Total length. -- Distance from tip of nose to tip of tail, not including the hairs. Mouse placed with its venter against a rule and stretched full length along it. Length recorded to the nearest millimeter.

Tail length. -- Distance from posterior limit of the two innominate bones to tip of tail, not including the hairs. Determined by pressing a specially designed rule against the skin covering the posterior faces of the bones. The rule had a small wooden block bolted on one end and set flush with the zero reading. The block was of such size as to make simultaneous contact with the two innominates without provoking excessive kicking. Length was recorded to the nearest millimeter. (Although the females of certain forms of peromyscus tend to have slightly longer innominates than do the males (Murie, 1933: 11-12), this fact is probably of little significance in the present study.)

Body length. -- Distance obtained by subtracting tail length from total length. Since tail length was slightly larger than when determined by the standard method, calculations of body length averaged somewhat smaller.

Hind-foot length. -- Distance from heel to tip of longest claw of left hind foot. Measured with a vernier caliper. Foot held straight between the thumb and index finger. Length recorded to nearest tenth of a millimeter.

Weight. -- Obtained by use of a laboratory balance. Recorded to nearest tenth of a gram.

Tail Amputation

Removal of the tail, a necessary part of several experiments, was accomplished by cutting across the tail, usually near its base, with sharp scissors which had been sterilized in 70 per cent alcohol. The severed part was measured to the nearest millimeter and the length of the stub calculated by subtracting the length of the detached portion from the original tail length.

Operations were of two kinds: (a) "half-tail" removal, in which the part removed equalled approximately one-half of the original tail and (b) "complete," in which a stub was left that was just visible as the mouse moved about. The length of the tail stub, measured from the posterior level of the innominates, averaged about 13 millimeters. All references, unless otherwise specified, are to complete tail removal.

Although most of the mice were anesthetized for the operation, no mouse was exposed to the ether fumes long enough to become more than partly inactive. This precaution was taken because at least one species of Peromyscus is particularly sensitive to ether fumes (Svihla, 1932: 14). Bleeding was slight. Amputees were placed immediately in clean cages, each mouse in a separate cage, and at least a month allowed before the animals were used. By that time the wounds had healed over completely.

Amputation of the tail appeared to have surprisingly little effect on the general behavior of the mice immediately following the operation. But their actions following release from their cages at the end of the convalescence period are of particular interest. When taken from their cages the animals were placed immediately on elevated platforms and forced to cross roughened glass tubes which they had learned to cross with considerable proficiency several weeks previously. The mice started across the tubes with no appreciably greater cautiousness nor appreciably less speed than shown immediately prior to the operation. Now considerably handicapped, they slipped more frequently and found it harder to right themselves when their hind feet slipped from the tubes. They appeared to be unaware of the cause of their difficulty in traveling upright and it was only after several slips that they began to travel more slowly and deliberately. This behavior, true to some extent of all of the mice, seemed to indicate that they were largely unaware of the loss of their tails. Possibly, life in the confined quarters of the small cages had made so few demands on tail use that the animals had either not become aware of the handicap or had so quickly learned to overcome it that they no longer recognized it. Certainly, their initial behavior on the climbing apparatus following tail amputation did not indicate noticeable awareness of the structural deficiency.

Experimental Rooms

Most of the experimental work was performed in two light-proofed reaction rooms in the Laboratory of Vertebrate Biology. Both rooms were provided with overhead lighting fixtures and wall switches, and the concrete floors were covered with a 1/2 - to 1-inch layer of sawdust.

The larger room measured approximately 9 by 21 feet, in inside dimensions, and was divided by a 2-foot-high, sheet-metal partition into two compartments, each approximately 9 by 10 1/2 feet. All corners were rounded by means of 2-foot-high, sheet-metal shields. Ventilation was provided by an electric fan, and passageways for the incoming and the outgoing air had light traps. There was a single door near one end, the opening guarded within by a 2-foot-high metal shield which prevented mice from escaping when the door was opened. The brick walls were heavily coated with smooth paint to a height of 2 feet to keep the mice from climbing them.

The smaller room measured approximately 7 by 8 feet, in inside dimensions, and its brick sides were painted to a height of 2 feet. There was a single door at the middle of one side, the opening provided with a smooth-painted wooden shield 18 inches high.

A few experiments were conducted in large metal drums located in a third room which was not light-proofed. Each drum was covered with a weighted wire-mesh lid which prevented escape of the mice and permitted adequate ventilation.

None of the rooms was soundproofed. There were only a few occasions, however, when experiments were discontinued temporarily because of excessive noise. Temperatures within the rooms varied approximately 30 degrees Fahrenheit over the period of study, but there was no indication that temperature differences affected in any way the experimental results.

HABITAT AND GENERAL BEHAVIOR

An extensive survey of the species of Peromyscus and their distribution over North America has been given by Osgood (1909). The brief descriptions given here are restricted to the ten forms covered by the present investigation. These accounts are concerned primarily with (a) the habitat preferences and terrestrio-arboreal habits and (b) the general behavior in captivity of the mice composing the stocks studied. Each of the ten forms studied differs somewhat in actions from each of the other forms. General behavioral characteristics, although frequently difficult of definition, affect in an important way the climbing activity of the mice and had to be taken into consideration not only in the evaluation of experimental results but also in the planning and conducting of the experiments. The descriptions of behavior are generalized and refer to the usual actions of the majority of individuals of the form. Within any form there will always be certain individuals which deviate considerably from the usual behavior pattern.

1. Peromyscus maniculatus bairdi. -- In various parts of its range inhabits prairie lands, open fields, and lake beaches, but everywhere seems to avoid forests (Dice, 1932: 4; Blair, 1940: 300-302). Largely terrestrial in habit, although Howard (1949: 12) reported that, under natural conditions, it occasionally climbs the bush clover (Lespedeza).

Bairdi mice tend to be timid and nervous. This is manifest in the relatively high frequency of hiding, trembling, chattering of teeth, cowering, and freezing when exposed to new surroundings. They explore cautiously and slowly at first and, even after they have become familiar with the new environment, perform very deliberately. They exhibit marked curiosity and considerable persistence in attempting difficult tasks.

2. Peromyscus maniculatus blandus. -- Occurs in habitats characterized by mesquite, creosote bush, atriplex, yucca, sumac, and other woody plants (Dice, 1930: 25; Blair, 1941: 225). Considered to be terrestrial in habit. No records are available to show that it climbs under natural, undisturbed conditions. Blandus, however, is actually capable of climbing the mesquite (W. F. Blair, personal communication), for an individual which escaped from one of Blair's traps, when chased, ran up into a mesquite bush and climbed about for several minutes before recapture. It is possible that the mouse could find no other retreat and behaved under stress quite contrary to normal. Even so, its behavior is obviously capable of modifiability.

Blandus mice are the least tractable of the ten forms. This conclusion does not agree with Svihla's (1932: 14), but it was the general opinion of workers in the Laboratory that the stock of blandus here described was very difficult to handle. These mice are nervous and highly excitable. When in strange surroundings they may remain perfectly motionless at the spot where placed or they may freeze, hide, run about in a rapid, jerky manner, or leap blindly in any direction. They were the least exploratory of the mice. Although fond of sunflower seeds, they rarely ate them during experiments of short duration.

3. Peromyscus maniculatus gracilis. -- Commonly associated with hardwood forest throughout its range. Although occasionally taken on lake beaches, in swampy regions, and in meadows, gracilis is seldom found any appreciable distance from forests (Dice and Sherman, 1922: 29-30; Dice, 1925a: 22-23; 1925b: 7) and is considered semiarboreal. Presumably, climbing plays an important role in the life of this form under natural conditions. Dice (1925b: 7) discovered three occupied nests under the rafters of a deserted dance pavilion. Johnson (1922: 37) captured an individual on the limb of a cedar tree about 4 feet from the ground. Van T. Harris (personal communication) recorded several instances in his field notes in which individuals climbed maple and beech trees when released from traps. Manville (1949: 32-33) noted their use of cavities in trees and stated that thirty-three climbed nearby trees when released from traps. One mouse ascended a hemlock about 30 feet before becoming lost to view. Among other trees climbed Manville mentioned oak, sugar maple, and basswood.

Gracilis mice are very tractable. Although they bite sharply and struggle vigorously when picked up, they become docile as soon as released. They explore new apparatus spontaneously and with apparent enthusiasm. Their movements are leisurely in contradistinction to the jerky movements of blandus or the more cautious, deliberate ones of bairdi. They exhibit marked curiosity and, even if they become momentarily excited, do not leap blindly from their positions.

4. Peromyscus maniculatus nebrascensis. -- Throughout its range limited fairly closely to sandhill country (Dice, 1941a: 1) characterized

by sparse vegetational covering. The vegetation is chiefly short grasses and yucca (B. T. Ostenson, personal communication), but a few shrubs, as sagebrush and rose, are present in parts of the range. Primarily terrestrial in habit. No records of climbing in nature are known to the writer and Ostenson (personal communication) found no evidence of it in the course of extensive field studies.

Nebrascensis mice are nervous and excitable but very curious and spontaneously exploratory. They sometimes freeze, or even jump blindly, when suddenly startled, but such behavior is usually followed almost immediately by a resumption of exploratory activity. These easily tamed mice showed so little fear of the observer's hands, often used to guide the mice toward a certain piece of apparatus, that they frequently climbed onto them and up her arms. This combination of fearlessness and curiosity made it difficult at times to direct the attention of the mice toward the desired object. On the floor they dug in the sawdust with relative frequency.

5. Peromyscus maniculatus oreas. -- Commonly associated with heavy coast forest characterized by such trees as Douglas fir, western hemlock, and red fir (Dice, 1949: 4, 22). Generally regarded as semiarboreal. Svihla (1933) found them inhabiting the dense underbrush of forests in the Olympic Peninsula of Washington. He recorded (1933: 13) an instance in which a mouse, upon escaping from a trap, ran rapidly to a nearby maple tree, and wrote: "I looked about hastily and accidentally glanced up into the tree. There, almost fifteen feet above me, was the mouse, climbing still higher with the ease and agility of a squirrel." Dalquest (1948) cited oreas as the only semiarboreal representative among six forms of Peromyscus occurring in Washington. He frequently caught oreas in traps set in trees for flying squirrels, and one individual was taken in a trap set 50 feet above ground.

Oreas mice behave in captivity very much like gracilis. The chief difference between them is that an oreas bites and struggles somewhat less when picked up and is even more leisurely and less excitable.

6. Peromyscus maniculatus rubidus (Hood River stock). -- Original mice of this stock trapped in cut-over land grown up to bushes and small trees, of which Douglas fir was dominant, a type of habitat intermediate between the heavily forested land which is the more usual home of rubidus and the adjacent areas of brushland inhabited by gambeli. A correlation of tail length with habitat among various stocks of rubidus was noted by Dice (1941b; 1949: 29). He found the tail of Hood River rubidus to be relatively shorter than that of several other stocks. Nothing is known to the writer regarding the role which climbing plays in the natural life of the Hood River rubidus, but presumably this brushland-inhabiting form is more or less intermediate in terrestrio-arboreal habits.

Rubidus mice, when held in the hand, struggle hard and sometimes bite, but they are not particularly excitable and constituted one of the more tractable of the forms.

7. Peromyscus polionotus leucocephalus. -- Occurring only on Santa Rosa Island, Florida, a beach-sand area. This is almost certainly

a strictly terrestrial form. No evidence of climbing has been reported for leucocephalus, although observations of its natural behavior have been made by several workers (Howell, 1920; Sumner, 1926; Hayne, 1950; Blair, 1951).

Leucocephalus mice are very excitable, jump readily upon occurrence of sudden sounds or movements, and are markedly hyperactive, moving rapidly from place to place in short, jerky runs. In spite of their excitability they can usually be trained without great difficulty by virtue of their spontaneous activity and very noticeable curiosity. They show marked persistence in repeatedly attempting difficult climbing feats. In their apparently fearless reaction toward the slow guiding movements of the observer's hands, they are somewhat like nebrascensis. Although many individuals climbed onto the hands, however, others took a more belligerent attitude. These mice boldly approached the hands and deliberately bit them or hit at them with one or both fore feet. This aggressive behavior was frequently accompanied by staccato squeaking. On the floor, like nebrascensis, they dug in the sawdust with relative frequency.

Along with the nervousness, or hyperactivity, of leucocephalus, and perhaps related to this activity, may be mentioned the relatively high frequency of face washing and the very noticeable cleanliness of the nests of this form. The nests are essentially hollow balls of cotton, and the cotton is kept clean and loosely fluffed out rather than being permitted to become matted down and soiled as is frequent with all of the other forms. It is interesting that the form which appears to be the most cleanly should also be the one to which marked personal cleanliness would presumably be most vitally important under natural conditions, for any concealing value which the predominantly white pelage of leucocephalus may have (Blair, 1951: 41) is dependent upon the continuous whiteness of that coat.

With reference again to the marked nervous activity of leucocephalus, it is possible that this activity, accompanied by the pronounced excitability of the form, plays an important role in escape from predators. A mouse running quickly in a straight line over an open expanse of sand could be overtaken readily by a more rapidly traveling predator. However, the tendency of leucocephalus to run rapidly in one direction for a short distance and then to turn suddenly and run in another direction, together with its tendency toward sudden leaping, might be expected, under certain circumstances, to confuse the predator to the extent of increasing the mouse's chances for survival. This same sort of zigzagging and sudden jumping is characteristic to a lesser extent of blandus and, to a still lesser extent, of nebrascensis, both of which inhabit relatively open country in many parts of their respective ranges.

8. Peromyscus leucopus noveboracensis. -- Occurs fairly generally throughout the hardwood forests of northeastern United States and eastern Canada and is almost entirely limited to wooded regions (Dice, 1937: 1; Burt, 1940: 16). Semiarboreal in habit. There is abundant evidence that they climb readily under natural conditions, and Nicholson (1941: 201-2) found, from a study of their use of nest boxes, that they actually prefer nest sites above the ground.

Although stocks from two widely separated parts of its range were used, the animals of both proved alike in behavior. Noveboracensis mice struggle very little and bite only rarely when picked up. They usually remain motionless and alert while being held and run or leap forward as soon as released. When pursued on the ground they run about in a rapid, excited manner. In running they tend to proceed directly from one landmark to another without pausing en route. When pursuit ceases they usually remain alertly motionless, ready to run forward at any moment. On elevated climbing equipment they generally remain motionless until urged into activity. Once aware of the part of the apparatus to be traversed, they perform unhesitatingly upon the slightest cue and by the most direct route available. Exploration of the apparatus is kept at a minimum.

9. Peromyscus nasutus nasutus. -- In the various parts of its range inhabits the yellow-pine association, the pinyon-juniper association, the rocky-slope association, or even the grassy-wash association (Dice, 1942: 205). It is found principally in regions characterized by rocks and brush or trees. The habitat is not limited to trees, but the mice seem to prefer them and are here classified as semiarboreal. Bailey (1931: 152), in describing the cliff-dwelling and tree-climbing habits of certain peromyscan mice of New Mexico, stated that the habits of nasutus are similar to those of P. boyli rowleyi. Since rowleyi is one of the most arboreal of all forms of peromyscus, Bailey apparently considered nasutus, likewise, to be somewhat arboreal under natural conditions.

Nasutus mice bite and struggle markedly when picked up, but are otherwise tractable. They explore leisurely and constitute one of the least excitable of the several forms. They are very much like oreas, for the most part, but are more curious and unlike them frequently resort to the apparently belligerent behavior of approaching, biting, and even hitting the observer's fingertips.

10. Peromyscus truei truei. -- Occurs most commonly in habitats containing such trees as yellow pine, pinyon, and juniper, although occasionally taken in grassland and certain desert regions (Dice, 1942: 205). Regarded as semiarboreal in habit. Their general type of habitat is similar to that of nasutus, and individuals of both forms are frequently taken in the same trap lines (Dice, 1942: 207). Observations of arboreal activity in truei were made by Bailey (1931: 152), who described their foraging activities not only along the bases of cliffs but also in the lower branches of nut-pine and juniper trees. He came upon one truei which lived in a nest of bark and sheep's wool located in the hollow trunk of a juniper tree. When not greatly disturbed, the mouse remained in its nest; but when alarmed, it climbed the smooth inside of the trunk with marked ease and agility. The type specimen was taken in a nest located 2 feet or more above the ground in the dead, hollow trunk of a small pinyon tree (Shufeldt, 1885: 403).

Truei mice usually struggle violently and bite sharply when picked up. They are markedly curious and spontaneously exploratory, and have, in general, little fear of slow, quiet movements of the observer. At times they are very tractable, at others, they behave in an excited manner, leaping suddenly and running rapidly. The excited activity of truei females with young has already been described by Svihla (1932: 14). Because of the unpredictability of the onset of excited activity, in individuals other than females with young, truei mice were particularly difficult to work with. Often they behaved very excitedly at first and, then, abruptly became fairly calm and docile. Sometimes the converse was true. Sometimes they failed to respond noticeably to strong stimuli, as the ringing of an alarm clock or a sudden movement; again they would respond markedly to weaker stimuli of similar nature. Sometimes the mice became suddenly excited for no apparent reason. Perhaps such unpredictable bursts of excitement in truei are correlated with special modifications of the sense organs. Possibly these mice are sensitive to a different range of stimuli than are the other forms of peromyscus studied.

Although no attempt to study modifications of the sense organs was made, the following observations suggest that certain modifications exist. Truei individuals upon several occasions went to the edge of an elevated platform and, with pinnae tensed, cocked their heads to listen to sounds made on the floor. Such individuals might listen to another mouse as it ran about on the floor or cracked the shell of a sunflower seed or might follow, as evidenced by head and ear movements, the observer's footsteps about the room. That a mouse was following the route of the observer by sound rather than sight was clear from the angle at which the head was held. This listening routine was manifested in its entirety only by truei, but members of other forms often executed certain phases of it. Truei seemed, too, to give overt response, either by ear twitching or other sudden change in behavior, to sounds of lower intensity than did the mice of the other forms. Whether a difference in auditory range or acuity actually existed is unknown, but truei was certainly keenly sensitive to sound and fairly good at localizing it. In this connection, the conspicuously large pinnae of this form are perhaps significant for, as Hoffmeister (1951: 34, 89-90) suggested, they may constitute an adaptation whereby truei, often living in regions where safe retreats are widely separated, may detect predators from afar and gain time in seeking refuge. Whether or not differences in vision exist among the various forms of peromyscus is also not known. The apparently larger size of the truei eye may be correlated with better vision, but observations of behavior made in the course of this study offer neither refutation nor support.

From the foregoing accounts it is apparent that most of the mice selected represented forms from two general types of natural habitat, terrestrial and semiarboreal, but one form came from a habitat of somewhat intermediate type. Those forms which live in nature in relatively open country are bairdi, blandus, nebrascensis, and leucocephalus, all of which are primarily terrestrial in habit as well as in habitat. Those which are semiarboreal both in habitat and habit are gracilis, oreas, noveboracensis, nasutus, and truei. The form which lives in brushland, a more or less intermediate habitat, is rubidus. Nothing is known about its terrestrio-arboreal habits. These ten forms represented five species. One of these species, maniculatus, included certain of the terrestrial (bairdi, blandus, nebrascensis) and semiarboreal (gracilis, oreas) forms as well as the form of intermediate habitat (rubidus).

In behavior the most tractable of the mice were the semiarboreal oreas, nasutus, and gracilis. Their behavior differed considerably from that of the other semiarboreal forms, noveboracensis and truei. Noveboracensis, ever tense and alert, gave the impression of performing in a direct, purposeful, and distinctly nonleisurely manner, whereas the enigmatic truei sometimes behaved in a most leisurely way and sometimes in a highly excited manner, its unpredictability at any given time being usually its most predictable characteristic. The intermediate rubidus, although less leisurely and exploratory than oreas, nasutus, and gracilis, was nevertheless tractable. The terrestrial forms showed various degrees of nervousness when exposed to new situations. Blandus, nebrascensis, and leucocephalus were especially excitable at such times. Nebrascensis lost its fear of new situations fairly readily; bairdi and leucocephalus lost theirs more slowly but then showed marked persistence in certain types of performance; and blandus was consistently least tractable. Additional characteristics of the mice studied included the marked cleanliness of leucocephalus and the digging tendencies of both nebrascensis and leucocephalus. All of the terrestrial forms did more digging than did any of the semiarboreal forms, but it was most frequently observed in these two forms.

CLIMBING BEHAVIOR

Use of Feet

In ascending tree trunks a peromyscus usually moves its feet one at a time, keeping three feet in contact with the trunk at any given instant (Pl. III, Q-T). Characteristically, the feet are moved forward in the following order: either fore foot, contralateral hind foot, ipselateral fore foot, contralateral hind foot. Although no records were kept of the number of instances in which the animals started forward with either the right foot or the left foot, there appeared to be no marked tendency to favor one side over the other in taking the first step. The feet, particularly the fore feet, are placed not directly under the body but somewhat to the side, the body remaining fairly close to the tree trunk. The main propulsive force seems to be exerted by the hind limbs, the fore limbs being used primarily in pulling the animal upward and then maintaining that forward motion. The toes are spread to some extent, and both the claws and the plantar tubercles are used in grasping the trunk. Although the feet are usually moved individually as the mice ascend trunks, in a few instances the animals moved their fore feet and their hind feet as pairs. A mouse ascending a trunk in this manner is shown in Plate III, U-X. This gait, which is more frequently observed among tree squirrels, was observed in a peromyscus only when the trunk climbed was one of relatively rough surface.

Descent of a tree trunk by a peromyscus is always head first (Pl. III, M-P). Both the feet and the toes are kept well separated. The mice tend to descend in an irregular spiral course, rather than directly downward. The spiraling is not shown in the figures, however, since, for photographic purposes, the mice were forced to descend the trunk along a narrow pathway. As descent is more difficult than ascent, the spiraling tends to distribute the weight of the mouse more at right angles to the line of gravitational pull and to reduce the tendency for the heavy posterior end of the body to roll outward and downward over the anterior end of the body. The oblique course also tends to reduce the degree of rotation required by the hind limbs in downward progression, so that more of the elongated plantar surfaces of the hind feet can be utilized to resist the downward pulling forces. In descent the feet are moved one at a time, three feet remaining in contact with the trunk as the fourth foot is moved to a new position. The maximum amount of rotation of the hind limbs seems to be about 120 degrees, whereas that observed in fox squirrels (Sciurus niger rufiventer) during the descent of tree trunks appears to be at least as great as 150 degrees.

In climbing along small branches the peromyscus usually keeps its toes spread well apart (Pls. IV, S; VI, A-L), although on very small branches the toes of the hind feet are sometimes held close together with their axes forming almost a right angle with the axis of the branch (Pl. IV, A-D). Both plantar surfaces and claws are used as the mice travel along the larger branches, but on branches of very small diameter the digital tips and claws often do not make contact with the branches. In sitting crosswise on a branch the mice usually keep the three middle toes of the hind feet fairly close together and spread the inner and outer toes of each hind foot. This manner of placing the toes is noticeable also when the mice travel more or less crosswise, as they occasionally do, along a branch of very small diameter or along a swaying branch of moderately small diameter.

The mice sometimes walk and sometimes run along horizontal branches. In progressing slowly the animals move their feet individually, keeping three feet in contact with the substratum at any given instant. The characteristic pattern of foot placement is illustrated in Plate VI, A-L. The order of raising the feet is as follows: either fore foot (left fore, A), contralateral hind foot (right hind, C and D), ipselateral fore foot (right fore, I), contralateral hind foot (left hind, L). As speed increases the mouse may continue to move its feet as described above (Pl. II, M-U), but with the occurrence of short intervals in which only two feet are simultaneously in contact with the substratum (Pl. II, M, N, Q). In traveling along a branch very rapidly, however, a mouse may break into a gait in which the hind feet are moved forward simultaneously, or almost so, and one fore foot is moved forward just before the hind feet strike the branch. In traveling rapidly along the ground or in running from a small branch onto a nearby support of considerable size, an animal may execute a half bound. In this type of gait the mouse raises its front feet, springs forward from its hind feet, and lands on first one fore foot and then the other, the first fore foot moving forward as the hind feet strike the substratum (Pl. II, B-K).

Use of Tail

In climbing peromyscus employs its tail as a prop, a balancing organ, a tactile organ, or a prehensile organ.

1. Prop. -- This use, in which the tail serves as a support, may be observed in a variety of situations. During ascent of a tree trunk a mouse usually holds its tail almost straight behind and close to the trunk. When ascent becomes arduous, the tail, pressed tightly against the trunk, helps to brace the weight of the animal. The proplike function of the tail is illustrated in Plate IV, U-V. Here the distal part of the tail is pressed against a projecting piece of bark, the animal having encountered (U) and then turned away from (V) a smooth-surfaced obstacle at the top of the trunk. In sitting crosswise on a small branch a mouse sometimes gains support by propping its tail against a nearby branch. On a fairly large branch an animal may employ its tail more or less like the third leg of a tripod, as it stands on its hind feet to wash its face or to investigate an overhanging object.

2. Balancing Organ. -- This use, in which the tail acts somewhat like the balancing pole of a tight-rope circus performer, is readily noted when a mouse travels along a flexible branch or along a nonflexible branch of moderately small diameter (Pls. III, B; IV, B-D). Under these conditions the mouse tends to keep its tail loosely flexed upward or behind, until balance becomes difficult; then the tail is tensed and waved conspicuously from side to side. As the weight of the mouse shifts too far to one side of the branch, the tail is waved toward the opposite side. If the entire tail is turned quickly to one side, movement of the posterior end of the body toward that same side may be rather sudden. If only the distal region of the tail is moved noticeably, movement of the hind quarters is considerably less abrupt. In general, the finer and more gradual shifts in balance are achieved by tail movements which do not appreciably involve the root of the tail. When balance becomes extremely difficult, however, the entire tail may be moved vigorously.

3. Tactile Organ. -- This use of the tail is particularly evident as a mouse travels about among small branches. The tail is waved gently behind in every direction. When it touches a branch, the tail is usually kept in contact with that branch, but not necessarily pressed against it or flexed over it, until the mouse has progressed so far forward that contact with it is lost. Should progression become difficult while the tail is in contact with a branch, the mouse will usually tighten the hold of its tail. Since employment of tail waving becomes more marked as locomotion becomes more difficult, the tail is most likely to encounter accessible branches at times when they can serve most effectively as an aid to locomotion (Pl. VII, U-X).

4. Prehensile Organ. -- A fourth function of the tail in scansorial activity is that of prehensility. No mouse was observed to hang by its tail, but as it travels along a hazardous pathway, flexing the tail over a nearby object enables the animal to brace itself somewhat as it seeks a secure foothold. In descending from one branch to another, a mouse can place its fore feet on the lower branch and then drop its hind feet toward the

same support while still maintaining its hold on the upper branch by means of the flexed tail (Pls. III, G-H; V, C-F, L-R; VII, G-K). The hold of the tail on the upper branch diminishes the rate of descent of the relatively heavy posterior part of the body and gives the animal more time to place its hind feet accurately below. When a mouse slips to the underside of a branch on which it is traveling, it almost always flexes its tail around that branch (Pls. III, D-F; IV, G-H). The flexed tail then helps to support the weight of the mouse as it clings to the underside of the branch and the tail may also serve to brace the animal in attempts to regain an upright position (Pl. IV, H; VI, M). In such an attempt, the flexing of only the distal region of the tail over the branch by the mouse permits the hind quarters greater freedom in making the appropriate righting movements.

EXPERIMENTS

I. Inclination to Climb

This experiment was designed to determine whether any of the forms of mice under study exhibited a natural aversion to climbing. The mice were offered an apparatus that all of them could climb easily and were given time to explore it freely. That the apparatus was actually well within the climbing ability of the mice was determined by preliminary observations of several extraexperimental representatives of each of the stocks studied, as well as by postexperimental observations in which individuals which did not climb during the experiment were found to climb the same apparatus readily when it afforded the only means of escaping from an area of confinement.

The apparatus (Pl. I, A) consisted of four elevated runways set at a height of 21 inches above four ground-level runways. The runways of each level radiated at right angles from a central support. The support was constructed of wood and provided with lath steps of such roughness and arrangement that any of the mice could easily climb to the top. The lower runways were roofed over with three-eighths-inch-mesh wire screen in such a manner that entrance to any runway could be gained only from the end adjacent to the central support. This made entrance to the lower runways comparable to that to the upper, there being only a single place of entrance to any runway and that next to the central support of the apparatus. Consequently, any mouse which explored a lower runway was necessarily made aware of the presence of the support which led upward, and no mouse which explored a lower runway could avoid the upper runways merely because random movements about the room did not lead it to the central support. All runways had metal sides and ends and were filled in with sand. The presence of tracks in the sand indicated the extent of exploration along the runways. The entire apparatus was placed on a flat baseboard which prevented in large measure the tracking into the runways of the sawdust covering the rest of the floor. Food, water, nesting material, and cover were all available in the vicinity of the apparatus in the middle of the room.

The number of mice tested was 80, 8 of each form. The sexes were equally divided. The mice were tested singly in a definite order as to stock and sex (the so-called "pairing method" of statistical usage). Each mouse was placed in the reaction room overnight and allowed free exploration. Since peromyscus is mostly nocturnal even in captivity (Johnson, 1926; Behney, 1936; Whitaker, 1940), each mouse was tested in total darkness -- the optimum condition for activity in blandus (Blair, 1943) and presumably for other forms of peromyscus as well. At the end of a test period the mouse was removed, its activity recorded, the sand smoothed over, and the food and water replenished. Each mouse remained in the reaction room approximately 24 hours.

TABLE I

Peromyscus Exploring Runways
at Each of Two Levels of Elevation

Species and Subspecies	Number of Mice Tested	Number of Mice which Explored One or More Runways at Ground Level	Number of Mice which Explored One or More Runways at Upper Level
Terrestrial:			
maniculatus bairdi	8	8	8
maniculatus blandus	8	8	5
maniculatus nebrascensis	8	8	7
polionotus leucocephalus .	8	8	7
Intermediate:			
maniculatus rubidus	8	8	8
Semiarboreal:			
maniculatus gracilis	8	8	7
maniculatus oreas	8	8	8
leucopus noveboracensis .	8	8	8
nasutus nasutus	8	8	8
truei truei.............	8	6	7
Total	80	78	73

The great majority of the mice explored at least one runway at each level of the apparatus (Table I). Of the 80 mice tested only two individuals, both belonging to the semiarboreal form truei, climbed to the runways of the upper level without exploring the lower level. Three blandus, one gracilis, one nebrascensis, one leucocephalus, and one truei failed to explore the upper level.

The difference between the total number of mice which explored at ground level and the total number which explored at the upper level was not statistically significant (chi-square equals 0.17, with 1 degree of freedom). The greatest difference within any one form in regard to exploration at both levels was shown by blandus, of which eight individuals explored at the ground level but only five climbed to the upper level. Here the chi-square value for the difference is 0.69, which still falls well above the 5 per cent level of probability. At neither level of the apparatus was absence of exploration correlated with either age or sex. Records kept of the number of mice exploring each individual runway at the two levels indicate that there were no directional preferences for any particular runway and that exploration of the several runways at a given level was at random.

The results of this experiment show that none of the ten forms of peromyscus tested were averse to climbing when the apparatus to be climbed was sufficiently easy and the mice were allowed to explore it freely. A few individuals, for reasons unknown, did not explore the apparatus at either one level or the other.

II. Reaction to High Places

In this experiment measurements were obtained of the reactions to high places of the ten forms under study. Reaction of mice to high places is an important factor in their climbing behavior, because such attributes as awareness of height, judgment of distance between branches, and fear of falling are involved.

The studies were conducted in the large reaction room. One compartment served as the experimental room proper and the other as an observation room. The two compartments were completely separated by a dark burlap curtain. The curtain was made into an effective one-way-vision screen by inserting an observation window of white cheesecloth in the center. The side of the burlap facing the experimental compartment was coated with white paint, and the cheesecloth facing the observation compartment was streaked with black paint to camouflage the outlines of the observer behind the screen. The experiment took place under dim light. During the early stages a 10-watt frosted bulb was used in the ceiling fixture of each compartment. That in the experimental compartment was later replaced by one of 15 watts because of difficulty in observing certain movements of the mice.

In the center of the experimental compartment was located a round elevated platform supported by a single metal rod. The platform measured 14 inches in diameter and its upper surface was 27 inches above the floor. A small, bottomless, wire-sided cage lined with transparent plastic sheeting was centered on the platform and a single sunflower seed placed under it. The roof of the cage was constructed of smoothly finished wood and was essentially a hinged door which could be readily locked when closed. With the door locked the entire cage could be lifted free from the platform (Pl. I, B) by means of a pulley mechanism operated from the observation compartment.

Testing procedure was as follows. Each mouse was removed from its own cage and transferred to the cage on the platform. The observer took up a position behind the curtain and set an interval timer for a seven-minute period. After two minutes, to give the mouse opportunity to become somewhat oriented to its new surroundings, the cage was raised to a specified distance (approximately 4 feet). The smooth transparent lining prevented the mouse from clinging to the sides of the cage and permitted observation of prior activity. As soon as the cage was raised the mouse was free to move about on the open elevated platform. The behavior of the unconfined animal was observed for five minutes, the length of the actual test. The mice were tested, insofar as practicable, in the same general order as in Experiment I. Ages varied considerably within each form and in some of the forms ranged from six weeks to three years. No correlation of age, or of sex, with any tested type of behavior was found.

TABLE II

Reaction of Peromyscus to Elevation on Open Platform

Mice permitted to explore freely for a five-minute test period.

Species and Subspecies	Number of Mice Tested	Number Remaining on Platform for Five Minutes	Percentage Remaining on Platform for Five Minutes
Terrestrial:			
maniculatus bairdi	17	10	59
maniculatus blandus	18	9	50
maniculatus nebrascensis	14	5	36
polionotus leucocephalus	14	5	36
Intermediate:			
maniculatus rubidus	12	8	67
Semiarboreal:			
maniculatus gracilis	18	15	83
maniculatus oreas	10	9	90
leucopus noveboracensis	10	10	100
nasutus nasutus	10	9	90
truei truei	16	8	50
Total	139	88	

The reactions of the mice to elevation on an open platform are given in Table II. The number (88) of mice which remained on the platform for five minutes is significantly greater than the number (51) which left it (chi-square for the difference equals 9.85, with 1 degree of freedom). The forms with the highest percentages of individuals remaining on the platform for the full test period were the semiarboreal noveboracensis, nasutus, oreas, and gracilis, and the lowest were the terrestrial leucocephalus and nebrascensis. Intermediate were the semiarboreal truei, the terrestrial blandus and bairdi, and the transitional rubidus.

Far more individuals of the semiarboreal forms, as a group, than of the terrestrial forms, as a group, remained on the platform for the five-minute period. Of the total number of individuals (64) in the semiarboreal group (18 gracilis, 10 oreas, 16 truei, 10 nasutus, and 10 noveboracensis), 51 stayed on the platform, whereas of the total (63) in the terrestrial group (14 leucocephalus, 14 nebrascensis, 18 blandus, and 17 bairdi), only 29 remained for the full period. The difference between these two groups in the relative numbers of mice remaining is highly significant statistically (chi-square equals 15.43, with 1 degree of freedom). Because of its intermediate natural habitat rubidus was not included in either the terrestrial or the semiarboreal category.

That the average length of time which the mice remained on the platform would have been much shorter had it been closer to the ground was demonstrated by the behavior of a control group. This group of 45 animals, representing all of the forms except noveboracensis, was tested under the same conditions previously described except that the platform was now located only an inch above the floor. Since no noveboracensis were available for controls, noveboracensis were not used in calculating the average time spent on the elevated platform by the semiarboreal mice. No member of the control group remained on the low platform for the full five minutes and the average time at which these mice left the platform was 0.51 minutes after the cage was raised. The average time which the controls remained on the platform was 0.64 minutes for the 22 terrestrial individuals and 0.37 minutes for the 19 semiarboreal ones. The average time spent on the elevated platform, on the other hand, was 3.10 minutes for the 63 terrestrial mice and 4.18 minutes for the 54 semiarboreal individuals. Since the terrestrial controls remained on the low platform longer, on the average, than did the semiarboreal, there seems to be no doubt that the tendency of the mice of the semiarboreal forms to remain longer on the open elevated platform than those of the terrestrial forms was due primarily to the greater elevation.

The data thus far presented show that in the absence of pathways to the ground semiarboreal mice are much more likely than terrestrial ones to remain on an elevated apparatus. The reaction to high places cannot, however, be regarded as a simple response, for the mice which left the elevated platform appeared to do so for diverse reasons. An analysis of their methods of reaching the ground is considered under four general categories: (1) running over the edge of the platform without giving evidence of previous awareness of the edge; (2) falling over the edge but evidently aware of its presence; (3) dropping from the edge deliberately; and (4) jumping from the edge deliberately. The proportion of mice using each method is given in Table III.

1. Running over Edge. -- Seven of the 139 mice tested ran off the platform almost immediately after the cage was raised without giving evidence of being aware of the presence of the edge. The action appeared accidental rather than deliberate, but was probably influenced by their excited state. Whether or not excitement was the main cause, however, is problematical, for some mice, particularly noveboracensis, although apparently highly excited, controlled their running in time to keep from

going headlong over the edge. Perhaps certain of the mice, despite a state of great excitement, were more alert to stimuli in the external environment than others which were equally excited. There is also the possibility that some individuals which appeared to be greatly excited were actually not so much so as others outwardly more calm.

There is no significant evidence that the excited behavior exhibited by the mice which ran over the edge was caused by their awareness of the elevated position. In the control group none of the 45 mice tested left the one-inch-high platform without first pausing at the edge and thereby giving evidence of awareness of the edge. That seven of the 139 individuals tested on the elevated platform ran off without any attempt at exploration or any noticeable previous awareness of the edge, whereas none of the 45 controls behaved similarly, may have been due to chance alone. The adjusted chi-square value for comparison of the difference between the number of mice running off the platform and the number not running off in the two tests is 1.18, with 1 degree of freedom. The adjustment used is that of Yates.

TABLE III

Methods of Reaching the Ground Employed by Peromyscus Which did Not Remain on Open, Elevated Platform for Full Five-minute Test Period

Species and Subspecies	Number of Mice which Ran off Platform	Number of Mice which Fell off Platform	Number of Mice which Dropped off Platform	Number of Mice which Jumped off Platform
Terrestrial:				
maniculatus bairdi	1	5	1	0
maniculatus blandus	2	7	0	0
maniculatus nebrascensis	0	8	1	0
polionotus leucocephalus .	2	6	1	0
Intermediate:				
maniculatus rubidus	1	1	0	2
Semiarboreal:				
maniculatus gracilis.....	0	2	1	0
maniculatus oreas.......	0	0	1	0
nasutus nasutus	0	1	0	0
truei truei..............	1	0	2	5
Total.............	7	30	7	7

Of the 139 mice, 1 of the 12 rubidus, 5 of the 63 terrestrial, and 1 of the 64 semiarboreal mice ran off the elevated platform during the five-minute test period (Table III). The adjusted chi-square value for the difference between the number of mice running off and the number not running off in the terrestrial and the semiarboreal groups is 1.62, which is not significant.

2. Falling over Edge. -- All of the 30 mice which reached the floor by falling off the platform appeared to do so accidentally rather than deliberately. Their behavior indicated that they recognized the presence of the edge of the platform, yet they slipped over despite this awareness. Several struggled hard to recover their lost footings, but fell anyway. A few seemed to lose their footholds at the edge as a result of rapid or jerky exploration. Many walked over the edge for no apparent reason whatsoever. Although two or three of the mice showed excitement, the animals which fell were not, as a whole, particularly excited. The characteristic which best distinguished those that fell, as a group, was their relative lack of exploration of what lay beyond the edge of the platform. Most of the mice explored to the extent of bringing the tips of their noses close to the edge, then failed to go close enough to look over it to the floor below. Whatever the reason for the low frequency of exploration, the mice probably would have been less likely to slip over the edge had they become more fully aware of its relationship to the ground. Another factor which seemed partly responsible for the falling of a few mice was clumsiness, but this may have been, at least to some extent, a manifestation of nervousness.

Among the mice which fell off there were far more representatives of terrestrial than semiarboreal forms. Twenty-six of the 63 terrestrial individuals tested fell over the edge, but only 3 of the 64 semiarboreal animals had that misfortune. One of the 12 rubidus also fell over the edge. Comparison of the terrestrial and the semiarboreal groups with respect to total numbers of individuals falling and not falling during the five-minute test period gives an adjusted chi-square value of 22.08, with 1 degree of freedom, which is highly significant. The semiarboreal mice are, therefore, shown to be far less likely than the terrestrial mice to fall off the elevated platform.

3. Dropping from Edge. -- All of the mice which dropped to the floor appeared to do so deliberately, as though well aware of the elevated position but anxious to leave the platform. In dropping the animals let themselves gradually over the edge until their heads and fore limbs hung free from the platform and only the plantar surfaces of their hind feet gripped the upper surface of the platform. Their tails were sometimes held in contact with the upper surface of the platform, but not always. The footwork required considerable rotation at the ankle joint as well as at the knee and hip joints. The rotation exhibited appeared to be similar, but perhaps less in degree, to that observed in squirrels descending tree trunks.

The mice appeared to recognize the general relationship of the platform to the floor. The majority in the course of exploration of the edge extended their heads well over it and looked down toward the ground; most of them recovered from at least one hind-foot hold before finally dropping. As a group they seemed excited but fairly cautious. Dropping in the described manner provided a method whereby the mice could get as close as possible to the floor before releasing their holds on the edge of the platform.

Of the mice which dropped to the floor three were terrestrial and four semiarboreal. The difference between the numbers of mice dropping and not dropping in the two groups gives an adjusted chi-square value of 0.0005, which is not significant.

4. Jumping from Edge. -- The seven mice which jumped to the floor seemed more excited than the mice which dropped. All individuals which jumped did so within a minute of the time the cage was raised and all appeared to jump deliberately. Although they explored very little before jumping, all of them paused at the edge and looked well over it toward the floor before leaving the platform. Jumping was always from the edge of the platform and the animals landed on the floor usually 2 to 4 feet from the base of the platform support. Their powerful jumps indicated that they recognized the platform to be well above the level of the floor.

Five of the mice which jumped belonged to the semiarboreal truei and two to the transitional form rubidus. Comparison of the terrestrial and semiarboreal groups with regard to numbers of mice jumping and not jumping gives an adjusted chi-square of 3.27, with 1 degree of freedom, which is not significant.

It seems particularly noteworthy, however, that the majority of the semiarboreal mice which left the platform during Experiment II did so deliberately, either by jumping or by dropping from the edge, and with awareness of the general relationship of the platform to the floor; whereas the majority of the terrestrial individuals left it accidentally, either by falling or by running from the edge, and with far less awareness of the elevation from the floor. Comparison of the semiarboreal and terrestrial groups with regard to numbers of individuals leaving the platform deliberately and those leaving it by accident gives an adjusted chi-square value of 15.01, which is highly significant.

Evidence that mice of the genus Peromyscus have an innate fear of falling is given by the large number (88) of mice remaining on the elevated platform for the full five-minute period, by the several recoveries attempted by mice which slipped accidentally over the edge, and by the many mice which took precautions toward making a safe landing before leaving the platform. Approximately half of the mice, furthermore, had never before been exposed to free exploration at any elevation greater than approximately 6 inches; yet the reaction to the elevated position of these mice, which had spent all of their lives in cages, differed in no apparent manner from that of the mice which had previously experienced considerably elevated positions. The dependency of an innate fear of falling upon the efficiency of the sensory mechanisms is known. In the terrestrial forms this fear seems to be less well-developed than in the semiarboreal and these forms may prove to be less sensitive to certain of the stimuli involved in the recognition of elevated position.

The results of this experiment show that mice of the forms tested differ in reaction to high places. The semiarboreal forms, gracilis, oreas, nasutus, truei, and noveboracensis, as a group, had a significantly greater tendency to remain on an elevated platform for the duration of a five-minute test period (79.7 per cent of the mice remained) than did the terrestrial forms, bairdi, blandus, nebrascensis, and leucocephalus, as a group (46.0 per cent remained). Rubidus, intermediate in habitat, was more or less intermediate between the semiarboreal and the terrestrial forms in reaction to elevation (66.7 per cent remained). The terrestrial mice were significantly more likely to fall from the platform than were the semiarboreal mice. Most of the semiarboreal individuals which left the platform during the test period seemed to do so intentionally, and they appeared to be well aware of the general relationship of the platform to the ground. On the contrary, most of the terrestrial mice which left the platform seemed to do so accidentally and with less awareness of the elevation. The experiment gives fairly good evidence that the mice tested have an innate fear of falling.

III. Climbing Vertically

The following three experiments were designed to test the ability of the mice to ascend upright objects.

1. Climbing Tree Trunks. -- In the first of these experiments selected sections of natural trunks were employed to ascertain the ability of the mice to climb trees of various kinds and sizes. The trunks were placed in the reaction room containing the two-level runway apparatus and the experiment conducted concomitantly with Experiment I. The number of trunks climbed as well as the number of runways explored were both recorded at the end of each test period. The tree trunks which were employed were those of Ailanthus glandulosa (tree of heaven), Fagus grandifolia (beech), Gleditsia triacanthos (honey locust), Acer negundo (box elder), and Ulmus americana (elm). Their heights and diameters are given in Table IV. The diameters were derived from circumference measurements taken 5 inches from the base, although each trunk was fairly uniform throughout its height. All trunks retained their natural coverings of bark throughout the experiment. The top of each section was completely covered with a layer of sand held in place by a peripheral ring of putty. Tracks in the sand were taken as indication that the mice had climbed to the top. Other conditions of the experiment have been described under Experiment I.

Mice of all the forms climbed a majority of the trunks offered (Table IV). The terrestrial blandus climbed the least total number of trunks (26) and the semiarboreal noveboracensis climbed the greatest (46). The total trunks climbed by blandus was significantly less than that climbed by either noveboracensis (chi-square equals 5.55, with 1 degree of freedom) or oreas (chi-square equals 4.19, with 1 degree of freedom), both semiarboreal forms. These were the only statistically significant comparisons obtained. The next greatest difference was that between the scores of blandus and truei, which gives a chi-square value of only 3.39.

A large majority of the mice climbed each of the following trunks: Ailanthus, Gleditsia, Acer, and Ulmus. All these were climbed in almost equal numbers by the mice, and the greater height of one of the two Ailanthus trunks proved no discouragement.

Mice of all of the forms showed a certain, some a very marked, degree

TABLE IV

Peromyscus Which Ascended Tree Trunks

Measurements of trunks recorded to nearest half inch.

Species and Subspecies	Number of Mice Tested	Number of Mice Which Climbed Each Kind of Trunk						Total Trunks Climbed
		Ailanthus (ht. 1'2"; diam. 9")	Ailanthus (ht. 3'½"; diam. 9")	Fagus (ht. 1'7½"; diam. 3")	Gleditsia (ht. 1'7"; diam. 5½")	Acer (ht. 3'10½"; diam. 10")	Ulmus (ht. 3'6½"; diam. 10½")	
Terrestrial:								
maniculatus bairdi	8	8	7	4	7	7	7	40
maniculatus blandus	8	5	4	0	5	6	6	26
maniculatus nebrascensis	8	8	8	2	7	8	7	40
polionotus leucocephalus .	8	7	8	0	7	8	8	38
Intermediate:								
maniculatus rubidus	8	7	7	3	7	7	7	38
Semiarboreal:								
maniculatus gracilis.....	8	7	7	4	7	7	7	39
maniculatus oreas.......	8	8	8	4	7	8	8	43
leucopus noveboracensis .	8	8	8	6	8	8	8	46
nasutus nasutus	8	6	7	3	7	8	7	38
truei truei.............	8	8	8	1	8	8	8	41
Total Mice which climbed each trunk		72	72	27	70	75	73	

of discrimination against the Fagus trunk. But, with the exception of blandus and leucocephalus, which are both terrestrial under natural conditions, all of the forms had at least one representative which climbed it. The form with the greatest number of representatives climbing the Fagus was the semiarboreal noveboracensis; six of these mice achieved such success. Comparison of the terrestrial forms, bairdi, blandus, nebrascensis, and leucocephalus, as a group, with the semiarboreal forms, gracilis, oreas, noveboracensis, nasutus, and truei, as a group, with regard to the relative number of mice which climbed the Fagus, gave an adjusted chi-square value of 6.76, with 1 degree of freedom; that is, significantly more semiarboreal than terrestrial mice climbed this trunk. Comparable chi-square values obtained by comparing rubidus with the terrestrial and the semiarboreal groups are 2.59 and 0.00, respectively, neither of the values indicating significance.

Of the 80 mice tested (8 from each of the 10 forms) only 27 climbed the Fagus, whereas at least 70 mice climbed each of the other trunks offered. In addition to the results given (Table IV), observation made clear that the smooth-, hard-barked trunk of Fagus was more difficult for mice of all of the forms to climb than were the rough-barked (Acer, Ulmus) or the soft-barked (Ailanthus, Gleditsia) trunks. That discrimination against Fagus was actually due to a difficulty in climbing rather than some other factor, such as odor, was confirmed many times. Moreover, none of the mice exhibited difficulty in climbing any of the other trunks listed (Table IV). Several times mice were seen struggling to to climb the Fagus. They reached well up onto the trunk with their fore feet, as though trying to get a firm hold on the bark; then, if they did not almost immediately give up the ascent apparently intended, they sometimes obtained a hold with one hind foot, only to fall back to the ground when attempting to place the other hind foot on the trunk. Frequently, a mouse would manage to grasp the trunk with all four feet, but would fall almost immediately in attempting to climb farther. That some of the mice were able to climb the Fagus more easily, however, was confirmed by observation as well as by the record.

As seen from Experiment I, all of the forms of mice tested had a natural tendency to climb, if an object presented was sufficiently easy and they were given ample time to explore freely. In the present experiment the Fagus trunk was the only one presented which proved markedly difficult for them. If Fagus is eliminated from the data of Table IV, there are no significant differences in the total numbers of trunks climbed by any of the several forms of mice. Again, the terrestrial blandus exhibits the lowest total climbing score (26 trunks climbed), but the difference between its score and the maximum score (40) attained by both truei and noveboracensis falls short of statistical significance (chi-square equals 2.97).

Supplemental material on trunk climbing was obtained by using trunks of two additional kinds. One was the hard-, rough-barked trunk of Prunus aucuparia (apricot). The section measured 14 inches in height and 4 1/2 in diameter. The Prunus trunk was added to the others in the experimental room for 10 successive 24-hour periods, while 10 mice, including a representative of each form, were tested. All of these individuals climbed the Prunus and all other trunks present except the Fagus, which was climbed by only two of them. The mice, therefore, were well able to climb the rough-barked Prunus despite the hardness of its bark.

Another trunk, introduced later, was from a tree of unknown genus. It was smoother than, but not quite so hard as, the Fagus. The section used measured 20 inches in height and 1 1/2 inches in diameter. It was left in the experimental room for 20 nights while two individuals of each form were tested. During the 20 test periods the mice showed noticeable discrimination against only two of the trunks, that of Fagus and that of unknown name. Of the 20 mice, 8 climbed Fagus, 7 climbed the unidentified trunk, and at least 14 climbed each of the other trunks. Of the mice which climbed the unidentified trunk there were two terrestrial and four semiarboreal , but the difference in the relative numbers of terrestrial and semiarboreal mice which climbed this trunk is not of statistical significance (chi-square equals 1.38). The results do suggest, however, that both smoothness and hardness of bark are factors which limit the trunk-climbing ability of the mice. A third factor which might be considered important is smaller diameter, but this was ruled out by evidence to be presented below (Experiment III, 2).

Observations of mice climbing the unidentified trunk were far fewer than for the Fagus, but in a few instances individuals were seen experiencing difficulty in climbing, or attempting in vain to climb, this trunk. The bark of this trunk, although a little softer than that of Fagus, was sufficiently hard to prevent ready penetration by the claws of the mice, and its excessive smoothness apparently offered a minimum of friction surface for effective grasping of the trunk by both the foot pads and the claws.

The results of this experiment show that all the peromyscus studied were well able to climb vertical trunks covered with bark which is either markedly rough (Acer, Ulmus, Prunus) or slightly rough and moderately soft (Ailanthus, Gleditsia), but that all of the mice had difficulty with trunks on which the bark was either very hard and only slightly rough (Fagus) or very smooth and fairly hard (unknown species). Furthermore, although all experienced difficulty in climbing the Fagus trunk, the semiarboreal mice experienced significantly less difficulty than did the terrestrial mice.

2. Climbing Tubes of Uniform Roughness but Progressively Greater Diameter. -- The second experiment of this group was designed to measure the comparative ability of the mice of the 10 forms to climb vertically on tubes of a given degree of roughness but which differed from one another in progressively greater diameter. Results of several preliminary tests indicated that, given tubes of uniform roughness, those of large diameter were more difficult for the animals to climb than those of small diameter; also, the tests showed that some individuals experienced greater difficulty than others.

Advantage was taken of the fact that the mice, when confined to small quarters devoid of hiding places, usually attempted to escape by any means at hand. In this experiment a tall glass cylinder of large diameter constituted the area of confinement and a vertical, axially located, roughened 2-foot glass tube the means of escape. Each mouse was trained for the experiment (see below) and the reward offered was escape from the narrow confines of the cylinder, with its lack of hiding places, to more roomy quarters outside, where a protective nest pan and an abundance of nesting material were available. Across the open top of the cylinder was placed a landing platform. The climbing mice were able to reach the platform easily from the vertical tube and could then travel down a gradually sloping pathway to the ground.

The eight tubes presented the mice were of the following outside diameters: 7.0, 19.3, 25.1, 30.0, 35.6, 40.0, 44.5, and 49.7 mm. A ninth tube of 63.4 mm. was also offered for a considerable period, but, since no mouse ever climbed it, its use was finally discontinued. The uniform degree of roughness of the outsides was furnished by covering the tubes evenly with 600-mesh Crystolon, a silicon carbide abrasive material ground to that size. Each tube was coated with brushing lacquer and then rolled immediately in the Crystolon. The covering was not only uniform but remarkably resistant to wear. Tubes were replaced whenever a surface became marred by feces.

Each tube was supported from within by a sturdy vertical support, secured to a horizontal baseboard, which centered the tube within the cylinder or jar. A tube could be readily slipped over the support and placed in proper position. The upper ends of the larger tubes were provided with corks to prevent the mice, when they climbed to the top, from falling into the tubes. In each jar was placed a 24-hour supply of food and water and sufficient cotton batting to enable a mouse to keep warm, but not enough to constitute a hiding place. A shallow layer of sawdust in the bottom of the cylinder served as a moisture absorbent. The space outside the jar was always larger than that within it and contained the standard food, with the addition of sunflower seeds, and a nest pan with sufficient cotton batting for a nest.

The 10 cylinders used ranged in height from 20 to 31 inches. In inside diameter they were approximately 8 1/2 to 11 1/2 inches. Four of the cylinders were made taller than the standard 20- and 24- inch heights by inserting linings of plastic sheeting which continued upward beyond the original tops. The tallest cylinders were resorted to in cases where jumping rather than climbing from a jar was suspected.

The experiment was conducted and scored as follows. A mouse was placed in a cylinder containing a vertical tree trunk of small diameter and of such roughness that any of the mice could easily climb it. Once a mouse had climbed from the cylinder and explored the space outside, the smallest tube in the series, the 7.0 mm., was substituted for the trunk and the mouse again placed in the cylinder. When the mouse had escaped by way of this tube, the next larger tube in the series, the 19.3 mm., was inserted and the mouse put back. This was repeated until the mouse, after a period of 24 consecutive hours, had still not escaped from the cylinder. Whichever tube was then in the jar was replaced by the tube next smaller to it, the food and water replenished, and the mouse closely observed. If it climbed the smaller tube, the next larger one, previously rejected, was returned and the mouse in due time was returned to the cylinder. If the animal again failed to climb the larger tube while being observed, but was absent from the cylinder later on, it was once more returned to the cylinder. It was always considered necessary to see the mouse in the act of climbing the critical tube in the series before scoring it as having done so, and it was also necessary to witness any futile attempts to climb the next larger tube in the series. No mouse was scored as having climbed a given tube unless it had climbed at least a foot upward along it. This distance was not accurately determined, however, until the limit of the climbing ability of the mouse was approached. Individual records kept for each mouse indicated the order in which the tubes were presented, the tubes apparently climbed, the tubes actually observed to have been climbed, and the tubes attempted in vain. The maximum number of different-diametered tubes which an animal was able to climb, as determined by direct observation with regard to the critical tube, represented its final tube-climbing score.

Some mice attempted to climb only at night, others as soon as they were placed in a cylinder, and still others had occasional daytime periods of wakefulness, in addition to their nocturnal activity periods, during which they would attempt to climb. The length of the test periods for the individual animals ranged from a single day to three weeks.

Although all of the mice learned to escape from the cylinder by climbing the tubes, a few at some advanced stage of the experiment developed a lack of inclination to do so. When this disinclination persisted, such individuals were eliminated without being scored. If a mouse which had succeeded in climbing a certain number of tubes attempted only weakly, or not at all, to climb the next in the series, it was rechecked to determine whether it was actually unable to climb the tube or had merely lost its incentive to escape. Rechecking was accomplished by reintroducing a means of escape well within the animal's demonstrated ability to climb. There is no evidence that elimination of the mice which had lost their incentive to climb affected in any way the experimental results. All of them had climbed at least one tube, and some several, before they were eliminated, and their climbing activity gave no indication that they differed in ability from other representatives of their respective forms.

A tendency to jump, rather than to climb, out of the cylinder, was exhibited by several of the mice. This was suppressed in large measure by the use of the tallest cylinders. A few mice, however, having once developed the habit of successful escape by jumping to the landing platform, could not be retrained in a reasonable length of time to escape by climbing even when one of the tallest jars was used. They would persist for a time in trying to jump to the top of the jar, but finally, after repeated failures, would settle down and make no further effort. Whenever a mouse could not be retrained to escape by climbing, it was eliminated from the experiment.

Since this experiment was conducted over a long period of time and in three different rooms, there were several variable factors. In view of the more or less comparable amount of variability, however, in each of the three rooms and because the mice were free to perform whenever conditions suited them, it seems likely that any environmental differences which existed were of negligible importance. Any slight effect the variables may have had was offset, furthermore, by the purely haphazard placement of a mouse in any particular room and by the proportional representation in any given location.

The mean climbing scores of the individuals tested in each form are listed, together with the means for body measurements and age in Table V. Since there were no significant differences in performance between males and females, the sexes have not been treated separately. Inspection of Column 3 of the table reveals the wide differences that existed among the forms in the mean number of tubes climbed. It is of particular interest that, in mean achievement, the four terrestrial forms, leucocephalus, blandus, bairdi, and nebrascensis, made the four lowest scores; the five semiarboreal forms, gracilis, truei, noveboracensis, nasutus, and oreas, the highest; and rubidus, from an intermediate type of habitat, an intermediate rank. Thus, the semiarboreal forms are demonstrably better able to climb tubes of greater diameter at the stated degree of roughness than are the terrestrial forms. The terrestrial forms climbed only the tubes of smallest diameters; rubidus climbed those of smallest diameters plus some of larger diameter; while the semiarboreal forms climbed not only the small tubes but nearly all of the larger ones as well.

In order to determine the significance of the different climbing abilities of the several forms of peromyscus tested, the mean climbing score of each form has been compared with that of every other form. The probability ratings of these comparisons, as determined by the use of t values, are given in Table VI. On the basis of the probability ratings, the peromyscus tested tend to arrange themselves into at least four general, somewhat overlapping, classes with regard to ability to climb the tubes of progressively greater diameter: (1) The terrestrial leucocephalus, which differs significantly from all other forms except blandus (also terrestrial). (2) The three terrestrial forms, blandus, bairdi, and nebrascensis. Two of them differ significantly from leucocephalus and all differ significantly from all the semiarboreal forms but not from rubidus. (3) Rubidus, which differs significantly both from the semiarboreal forms and from leucocephalus. This significance reaches the 1 per cent level of probability, however, only in comparison with two means, one at each end of the range of means. In general, rubidus, in this particular experiment, tends to align itself more closely with the terrestrial than with the semiarboreal forms. (4) The semiarboreal forms, gracilis, oreas, noveboracensis, truei, and nasutus, all of which differ significantly from all of the terrestrial forms tested, as well as from rubidus. There can be no doubt, therefore, that the differences in tested climbing ability between the semiarboreal and the terrestrial forms are of considerable magnitude.

Correlation of tube-climbing ability of the total number of mice tested (83) with body length, tail length, foot length, weight, and age gives r values of .70, .81, .77, .59, and -.01, respectively. All of these correlations, except that of ability with age, are highly significant. The

TABLE V

Means and Standard Errors for Tube-climbing Ability, Body Measurements, and Age of Peromyscus that Climbed Tubes of Uniform Roughness but Varying Diameter

Body dimensions recorded in millimeters; weight, in grams; and age, in weeks.

Species and Subspecies	Number of Mice Tested	Number of Tubes Climbed	Body Length	Tail Length	Tail Length/ Body Length	Foot Length	Foot Length/ Body Length	Weight	Age
polionotus leucocephalus . . .	10	3.1±0.28	79.80±1.36	55.10±0.92	0.69	18.34±0.23	0.23	13.6±0.55	61.2±10.32
maniculatus blandus	7	4.3±0.61	93.00±2.04	66.29±2.00	0.71	19.97±0.27	0.21	21.1±1.13	64.7±12.28
maniculatus bairdi.	11	5.2±0.38	87.82±1.07	72.45±0.76	0.82	18.53±0.14	0.21	19.1±0.98	82.5±11.80
maniculatus nebrascensis . . .	8	5.3±0.31	88.13±1.25	66.88±1.86	0.76	19.29±0.18	0.22	19.4±0.79	67.1±8.40
maniculatus rubidus	8	6.0±0.57	88.50±2.69	90.88±1.57	1.03	20.46±0.25	0.23	18.6±0.81	84.8±21.12
maniculatus gracilis	9	7.6±0.24	95.33±1.68	99.33±1.89	1.04	21.46±0.20	0.23	22.4±0.98	69.2±8.64
truei truei.	7	7.7±0.15	96.86±1.26	91.29±3.80†	0.94†	22.17±0.20	0.23	25.7±0.76	41.4±13.78
leucopus noveboracensis. .	7	7.9±0.14	98.00±2.52	97.86±2.23†	1.00†	21.33±0.34	0.22	22.6±1.10	69.1±19.65
maniculatus oreas	6	8.0±0.00	93.33±1.12	110.17±2.89	1.18	23.18±0.18	0.25	22.3±1.07	53.7±12.86
nasutus nasutus	10	8.0±0.00	99.80±1.11	107.50±4.73†	1.08†	22.79±0.14	0.23	29.2±1.42	85.4±17.09

† Measurement includes one or more mice with incomplete tails.

TABLE VI

Probability Ratings for Comparisons of Mean Tube-climbing Scores (Table V) of Peromyscus

The probability that any two means represent two populations of the same mean climbing ability is read in the block connecting the names of the two forms considered. 0 indicates a probability greater than .05 (not significant); * indicates a probability of .05 to .01 (significant); and ** indicates a probability of .01 or less (highly significant).

Species and Subspecies	p. leucocephalus	m. blandus	m. bairdi	m. nebrascensis	m. rubidus	m. gracilis	t. truei	l. noveboracensis	m. oreas	n. nasutus
polionotus leucocephalus....	...	0	**	**	**	**	**	**	**	**
maniculatus blandus........	0	...	0	0	0	**	**	**	**	**
maniculatus bairdi.........	**	0	...	0	0	**	**	**	**	**
maniculatus nebrascensis...	**	0	0	...	0	**	**	**	**	**
maniculatus rubidus........	**	0	0	0	...	*	*	*	*	**
maniculatus gracilis	**	**	**	**	*	...	0	0	0	0
truei truei	**	**	**	**	*	0	...	0	0	0
leucopus noveboracensis....	**	**	**	**	*	0	0	...	0	0
maniculatus oreas	**	**	**	**	*	0	0	0	...	0
nasutus nasutus	**	**	**	**	**	0	0	0	0	...

correlation of body length with climbing ability seems to be an important one, particularly with respect to span; for in general the longer the body, the longer the appendages. As long appendages can reach farther around the large tubes than can short appendages, the long-limbed mouse is better able to embrace the tube. Observations confirmed that a long-bodied, long-limbed nasutus is able to reach considerably farther around a tube of large diameter than is a relatively short-bodied, short-limbed leucocephalus, which cannot utilize as large an arc as nasutus and is unable, therefore, to brace its body as firmly against the tube. In effect, leucocephalus is required to climb a flatter surface than is nasutus.

Although the tail was pressed closely against the tube during difficult ascent, somewhat as a prop, there is no evidence that such use of the tail affected appreciably the tube-climbing scores of the mice. Twenty mice, two from each form, were tested with their tails and later retested without them. The 20 mice climbed 127 tubes before tail removal and a total of 115 tubes afterward. As a check, nine other mice, including an individual of each form except truei, were tested and retested in the same manner but with their tails intact in both tests. The nine mice climbed 57 tubes in the first test and 56 in the second. The difference in the numbers of tubes climbed by each group in the two tests is not statistically significant (chi-square equals 0.13). It seems unlikely, therefore, that the tube climbing was much affected by the tail lengths despite the very high correlation (r equals .81) between ability and length of tail.

Presumably, a long foot presents a greater grasping surface than a short foot; and a foot which is not only absolutely longer but relatively longer should be of still greater advantage in grasping. The highly significant correlation (.77) of climbing ability with absolute foot length has already been noted. The r value for correlation of climbing ability with the foot length-body length ratio in all individuals of the 10 forms is only .11, which, although positive, falls considerably short of significance. The corresponding r value for all individuals (49) of the six subspecies of maniculatus, however, is .32, which is of statistical significance.

That foot length and demonstrated climbing ability are here more closely correlated (r equals .77) than are body length and climbing ability (r equals .70) may be due to chance. It suggests, however, either that the demonstrated ability is dependent even more on absolute foot length than it is on absolute body length or that the size of both body length and foot length is controlled in large measure by general growth factors. Since few mice were tested and the measurements used do not lend themselves well to the determination of general or local growth factors, it can be stated here only that a highly significant correlation exists between demonstrated climbing ability and both absolute body length and absolute foot length.

The role of weight in climbing performance is difficult to ascertain. The weights of the mice used fall within the range considered normal for their forms as reared under laboratory conditions. When all individuals of the 10 forms are lumped in making the determination, the correlation value (.59) between weight and the number of tubes climbed is highly significant. Within a few of the forms there is evidence of a negative correlation. This attained significance only in bairdi, in which it amounted to —.69. Weight and body size have a general correlation in peromyscus (Table V), as in most animals, and mice of the forms with large body size usually demonstrated greater climbing ability than did those with small size. Consequently, it may be that the high correlation between weight and climbing ability (mice of all 10 forms lumped together) was due primarily to the dependence of weight on body size and that, if all other factors could be made equal, the less heavy of two mice would attain the higher performance score. For example, a particular leucocephalus, because of its relatively small size rather than its light weight, might be less able than a nasutus to climb a certain tube; but this same leucocephalus, chiefly because of its lighter weight, might be better able to climb the specified tube than another leucocephalus of the same body dimensions but greater weight.

Because of the general nature of this experiment the relative importance of body length, tail length, foot length, and weight in the climbing performance of an individual mouse cannot be determined. Each form is represented by only a small number of individuals; there is considerable individual variation in most of the measurements employed; and climbing ability depends on not one, but many, interdependent and diverse factors. The lumping together of the several forms is justified only in the determination of certain general correlations, for different species exhibit differences in body proportions other than those involving foot length and tail length (Clark, 1941). The lumping together of individuals of different subspecies of the same species is open to the same criticism, even though the number of significant subspecific differences in body proportions may be assumed to be less than the number of significant differences in body proportions that distinguish the species.

In conclusion, it may be stated that, whatever the relationship of body proportions to the type of climbing ability tested is, and it is highly complex, all of the semiarboreal forms proved better able to climb the tubes of greater diameter at the selected degree of roughness than did the terrestrial. Each semiarboreal form tested achieved a mean climbing score significantly higher than that of any terrestrial form. Rubidus, the intermediate in habitat, was intermediate also in climbing ability.

3. Climbing Tubes of Uniform Diameter but Progressively Lesser Roughness. -- The third experiment of this group, which is very similar to the second, was designed to measure the comparative ability of the mice to climb vertically on tubes which differed from one another only in degree of roughness. Evidence that roughness of surface affects the performance of mice was given in the trunk-climbing experiment above as well as in preliminary tests which involved the use of roughened tubes. The conditions and apparatus were the same as those in the second of these experiments except for the use of a different series of tubes. The four tubes employed in scoring each measured 44.5 mm. in diameter, but represented a graded series of progressively decreasing roughness. This was achieved by covering the tubes with 150-, 220-, 320-, and 600-mesh Crystolon, respectively. The 600-mesh, which is the

most finely powdered Crystolon, is comparable in fineness to dusting powder. The mice tested, for the most part, were the same as those of the preceding experiment. A few animals, for reasons due entirely to chance, were used in only one of the two experiments.

The results of this experiment, presented in Table VII, are remarkably similar to those of the preceding one (see Table V). Although the progressive order of mean achievement differs somewhat in the two experiments, the four terrestrial forms, as before, made the four lowest scores, the five semiarboreal made the highest scores, with rubidus maintaining its intermediate position. The probability ratings obtained by comparing the several performance means are given in Table VIII. As in the prior experiment the ratings fall into four groups: (1) Leucocephalus, in which the mean climbing score differs significantly from the mean scores of all other forms except nebrascensis and blandus. (2) Nebrascensis, blandus, and bairdi, all of which differ significantly from all of the semiarboreal forms in mean performance and one of which (bairdi) differs also from leucocephalus. A difference significant at the 5 per cent level exists also between the means of nebrascensis and rubidus. (3) Rubidus, which differs significantly in mean performance from all other forms but blandus and bairdi. This significance, however, barely reaches the 1 per cent level when considered with reference to the semiarboreal forms oreas, noveboracensis, and truei, and is between the 5 and the 1 per cent levels with reference to the terrestrial nebrascensis. (4) Gracilis, oreas, noveboracensis, truei, and nasutus, the performance means of which differ very significantly from those of all of the other forms. Mice of the semiarboreal forms, then, may be said to have demonstrated markedly greater ability to climb the relatively smooth-surfaced tubes than do those of any of the other forms.

Just as in the preceding experiment, highly significant positive correlations exist between demonstrated ability and body length, tail length, foot length, and weight, respectively, when all individuals of the 10 forms are lumped together in determining the correlations. The general agreement of correlation trends in the two experiments is not unexpected inasmuch as the mean body measurements and the comparative abilities, as indicated by statistically significant differences in performance means, are very similar.

Some general conclusions to be drawn from the results of the two tube-climbing experiments are (a) that the ability in forms of peromyscus to climb vertically placed objects is limited by both progressively larger diameter and progressively greater smoothness of surface of those objects and (b) that vertical-climbing ability in the forms studied is definitely correlated with the general type of natural habitat and presumably also with the general type of natural habit. Mice of the semiarboreal forms, therefore, should be better able to climb a greater variety of objects in nature than terrestrial mice, and rubidus individuals should be neither so able as the semiarboreal mice nor so unable as the terrestrial ones.

TABLE VII

Means and Standard Errors for Tube-climbing Ability, Body Measurements, and Age of Peromyscus that Climbed Tubes of Uniform Diameter but Varying Roughness

Body dimensions in millimeters; weight in grams; and age in weeks.

Species and Subspecies	Number of Mice Tested	Number of Tubes Climbed	Body Length	Tail Length	Tail Length/ Body Length	Foot Length	Foot Length/ Body Length	Weight	Age
polionotus leucocephalus...	10	1.8±0.10	79.50±1.37	55.00±0.79	0.69	18.35±0.19	0.23	13.6±0.65	50.2±11.34
maniculatus nebrascensis ...	8	2.1±0.23	87.75±1.56	66.50±1.95	0.76	19.21±0.21	0.22	18.9±0.94	66.0±9.47
maniculatus blandus	7	2.1±0.34	90.86±2.67	68.71±1.66	0.76	20.16±0.30	0.22	20.8±1.43	52.6±11.23
maniculatus bairdi..........	12	2.4±0.19	88.00±1.35	71.50±0.88	0.81	18.29±0.12	0.21	19.4±0.97	92.1±12.15
maniculatus rubidus	9	3.0±0.29	90.89±2.28	92.33±1.70	1.02	20.67±0.90	0.23	20.2±1.18	94.3±18.16
maniculatus gracilis........	11	3.9±0.09	94.82±1.37	98.36±1.71	1.04	21.45±0.16	0.23	22.9±0.88	63.8±8.15
maniculatus oreas..........	7	4.0±0.00	93.57±1.04	111.86±3.05	1.20	23.33±0.16	0.25	23.4±1.46	52.0±11.50
truei truei...........	7	4.0±0.00	96.86±1.06	90.43±3.36†	0.93†	22.47±0.23	0.23	24.7±0.78	48.4±16.26
leucopus noveboracensis..	7	4.0±0.00	99.43±2.45	97.57±1.69†	0.98†	21.23±0.32	0.21	22.6±1.10	71.3±19.12
nasutus nasutus	10	4.0±0.00	99.80±1.11	107.50±4.73†	1.08†	22.79±0.14	0.23	29.2±1.42	86.0±17.09

†Measurement includes one or more mice with incomplete tails.

TABLE VIII

Probability Ratings for Comparisons of Mean Tube-climbing Scores (Table VII) of Peromyscus

The probability that any two means represent two populations of the same mean climbing ability is read in the block connecting the names of the two forms considered. 0 indicates a probability greater than .05 (not significant); * indicates a probability of .05 to .01 (significant); and ** indicates a probability of .01 or less (highly significant).

Species and Subspecies	p. leucocephalus	m. nebrascensis	m. blandus	m. bairdi	m. rubidus	m. gracilis	m. oreas	t. truei	l. noveboracensis	n. nasutus
polionotus leucocephalus....	...	0	0	*	**	**	**	**	**	**
maniculatus nebrascensis...	0	...	0	0	*	**	**	**	**	**
maniculatus blandus........	0	0	...	0	0	**	**	**	**	**
maniculatus bairdi	*	0	0	...	0	**	**	**	**	**
maniculatus rubidus........	**	*	0	0	...	**	**	**	**	**
maniculatus gracilis	**	**	**	**	**	...	0	0	0	0
maniculatus oreas	**	**	**	**	**	0	...	0	0	0
truei truei	**	**	**	**	**	0	0	...	0	0
leucopus noveboracensis....	**	**	**	**	**	0	0	0	...	0
nasutus nasutus............	**	**	**	**	**	0	0	0	0	...

IV. Crossing of Gaps

1. Reaching across Gaps. -- Observation of the methods by which the mice crossed open spaces at elevated levels showed that if the gap was small and the mice had had no previous experience in crossing it, they usually reached across from one support to another. As the gap became larger and spanning it became more difficult, the mice jumped it when forced to make the crossing. Because of the tendency of the mice to jump gaps which were difficult but not necessarily impossible for them to reach across, the data on maximum reach are relatively few.

Horizontal Reach. Measurements of maximum horizontal reach were obtained by training the mice to cross successively larger gaps between two parallel rods. Each rod was of unpolished wood and one-fourth of an inch in diameter. Just prior to spanning the gap between the two rods a mouse would stand with all four feet on one rod and stretch its head forward toward the other, moving its vibrissae noticeably. In crossing, a mouse usually placed its feet individually as in walking. The tail was not used as a prehensile organ but to help the animal balance on one rod while stretching forward toward the other.

The maximum horizontal reach of the 11 mice tested, representing seven of the forms, ranged from 6.5 to 8.5 cm. as measured at 5-mm. intervals. It averaged 7.0 cm. for the four terrestrial individuals and 7.6 cm. for the seven semiarboreal. In no instance was the reach greater than the body length of the mouse, averaging 83 per cent of the body length in the 11 mice tested. In the terrestrial mice it averaged 79 per cent of the body length; in the semiarboreal, 86 per cent. Both absolute and relative horizontal reach, then, are greater in the semiarboreal than in the terrestrial for the individuals tested.

Downward Reach. Measurement of maximum downward reach was obtained by using two glass tubes of 7 mm. in diameter roughened externally with 220-mesh Crystolon. The tubes were set so that the tip of the upper was directly above the tip of the lower and so placed that the mouse had to proceed well toward the tip of the first tube in order to reach down to the second. The lower tube was terminated by a wooden cylinder, roughened by applying two rings of adhesive tape. This cylinder, approximately 35 mm. in length and 15 mm. in diameter, served as the landing platform toward which the mouse reached from above. The gap between the axes of the tubes was progressively increased by 15 mm. intervals. When a mouse reached down with its forefeet, it continued to hold on to the upper tube with its hind feet and, on the greater reaches, it flexed its tail about the upper tube. The apparatus and the downward reaching of the mouse are illustrated in Plate VII, A-T.

The maximum downward reach of the 11 fully tailed mice tested, representing all the 10 forms, ranged from 7.0 to 11.5 cm., as measured at 15 mm. intervals. It averaged 8.1 cm. for the four terrestrial individuals and 10.7 cm. for the six semiarboreal mice, and was 8.5 cm. for the single rubidus. The performance of an additional mouse, a gracilis with amputated tail, gave a value of only 7.0 cm. The maximum reach of the tailless gracilis was 1.1 cm. below the average for the four terrestrial mice, 3.7 cm. below the average for the six semiarboreal, and 4.5 cm. below the maximum reach of its tailed littermate of the same sex. Although these results are based on a very small number of mice, they do suggest that tail length is of considerable importance in assisting the mice to descend from one tube to another.

The maximum downward reach of the 11 tailed mice averaged 1.06 times their respective body lengths. The ratio of maximum reach to body length averaged 1.13 in the six semiarboreal individuals and 0.98 in the four terrestrial, and was 0.96 for the single rubidus and 0.80 for the single tailless gracilis. The tailless mouse had the lowest of any of the individual ratios. The maximum downward reach is shown, therefore, to be greater, in both absolute and relative terms, than is the maximum horizontal reach of the mice. When the animals hang downward from the upper support, while reaching toward the lower, they are obviously able to span greater gaps than when reaching forward across the space between horizontal rods.

In reaching toward the lower support with their forefeet the mice hung on to the upper one with their hind feet, assisted by their flexed tails. As soon as the forefeet had made secure contact below, an animal released its foothold above. It then made use of its tail to retard the rate of falling of the hind quarters by maintaining a gradually diminishing hold on the upper support (Pl. VII, G-K). The performance of the mice shown in Plates V, C-F, L-R, and VII, E-K, in comparison with that of the mouse shown in Plate III, F-K, gives some idea of the greater effectiveness of a relatively long tail, as distinguished from a shorter one, as an aid to successful descent in peromyscus. The longer tail not only renders the dropping of the hind quarters of the mouse more gradual, but facilitates more accurate placement of the hind feet on the lower support.

In reaching downward across small gaps the mice placed their four feet one after the other on the lower support, the two forefeet being usually followed by the two hind feet (Pl. VII, N-T). In the spanning of large gaps, however, both hind feet were released almost simultaneously from the upper support once the forefeet had taken hold of the lower one (Pl. VII, I-K).

Upward Reach. No measurements were made of maximum upward reach, but it was observed that some of the mice, when reaching directly or almost directly upward, could span gaps which slightly exceeded body length. The mice stood on their hind feet and thus gained height. The tail usually functioned here like the third leg of a tripod, to maintain balance, as the animal stood on its hind feet and stretched upward with its forefeet.

In crossing from one to another of two supports the mice behaved very cautiously, particularly so if the gap to be spanned was approximately more than half the body length of the mouse concerned. Crossing of larger gaps was always preceded by investigatory movements of the vibrissae, and often the mouse repeatedly extended a forefoot toward the second support before it finally made the crossing. Most of the mice returned to the first support several times before they demonstrated their maximum reaching ability, and it was usually only under compulsion that the larger reaches were made.

2. Jumping across Gaps. -- Although the mice could be trained to jump considerable distances from one support to another, they did surprisingly little spontaneous jumping under the experimental conditions. Their exploration of artificial and natural branches was usually cautious. In progressing along branches the mice often reached from one branch to another, but rarely jumped unless trained to do so. Nelson (1918: 524) reported that he had several times observed mice of the genus Peromyscus running up and down the branches of a small leafless tree and "leaping from twig to twig with all the active grace of tiny squirrels." He wrote that they "appeared to be racing about in pure playful enjoyment of the exercise." None of the peromyscus studied here exhibited any such squirrel-like behavior and it seems more likely that under natural conditions the mice jump from branch to branch only in emergencies.

The instances of spontaneous jumping observed in the laboratory occurred for the most part either when the mice were attempting to escape from some piece of apparatus or when they were greatly excited. Occasionally, mice jumped from elevated apparatus, often directly toward a nearby object. Most other jumping observed, however, was by the mice confined to the tall laboratory cylinders in the tube-climbing experiments. The most spectacular jumps were made by two mice (one truei and the other blandus), both of which jumped 30 inches upward to the rim of a glass cylinder only 8 1/2 inches in inside diameter.

In one instance a leucocephalus jumped accurately a 5-inch distance from the top of an aluminum igloo to the upper edge of a vertically placed piece of transparent plastic sheeting 1 mm. thick. The mouse made a perfect landing midway between two paper clips fastened to the sheeting. (It is possible that the clips, which were about 4 inches apart, served as visual guides.) The edge of the plastic sheeting was about 2 1/2 inches higher than the top of the igloo. In another instance a blandus jumped horizontally from a wooden block to the adhesive-tape-covered rim, approximately 6 mm. thick, of a laboratory cylinder. The animal jumped 5 1/2 inches and landed perfectly. Later, when the cylinder was moved a little farther away, the mouse made a similar jump of 6 inches. Jumps toward larger objects were more common, however, and several mice were seen to jump from an elevated object onto a nearby brick wall or onto a large-diametered tree trunk. These jumps, observed in both noveboracensis and gracilis, averaged about a foot in distance and were made either slightly upward or slightly downward.

Despite the instances described, spontaneous jumping was relatively infrequent. Nevertheless, mice of all the forms could be trained to jump. The training procedure entailed progressively increasing the distance between two supports, initially placed close together so that the mice could easily reach from one to the other. As the distance between the supports was made successively greater, at some point the mice resorted to jumping across the gap. Experiments using two unpolished wooden rods of 1/4-inch diameter showed that the mice could be readily trained to jump upward or downward as well as horizontally. No attempt was made to determine the maximum jump upward or downward at various angles, but measurements were made of the maximum horizontal jump for at least one individual of each form.

The apparatus employed in determining the maximum horizontal jumps of the mice consisted essentially of two parallel wooden rods, each 6 inches long and one-fourth of an inch in diameter. The rods were 28 inches above the floor, and each rod was attached to an elevated platform. On each of the platforms was placed an igloo baited with a sunflower seed.

The animals were tested in dim light, a single 10-watt bulb in an overhead ceiling fixture. At the beginning of each test the rods were placed close together, with axes parallel, at a distance of 2 cm. A mouse was placed under an igloo. After two minutes the igloo was slowly raised and very little time was usually required for the mouse, in exploring, to walk or run from one rod to the other. The igloo was then returned to the first platform, the sunflower seed replaced if eaten, and the rods moved 5 mm. farther apart. Since this procedure was performed repeatedly it soon became so familiar to the mouse that it usually went directly to the starting rod upon raising of the igloo and crossed over. As the distance between the rods became appreciably greater the mouse resorted to jumping from rod to rod. Once the mouse had learned to jump across the gap, it was possible, as long as the distance was easily jumped by the mouse, to increase the distance between rods by more than 5 mm. each time. The exact amount of increase between rods on successive crossings depended upon the performance of the individual. When a certain distance was jumped with difficulty, thereafter the distance was never increased by more than 5 mm. Whenever a mouse fell in attempting a jump, the rods were again placed close together and the mouse once more presented with a series of successively greater reaching and jumping distances. When the mouse had thrice worked up to distances so great that it fell to the ground, either in jumping short of the second rod or in slipping from the second rod in attempting to land, the test was discontinued for that day. This procedure was repeated on successive days until it was certain that the animal had demonstrated its maximum, or very close to its maximum, jumping ability. In the mice tested, it required from 5 to 15 days of this training before the maximum jump was attained. The range of actual test days was from 10 to 17.

Considerable variability in the behavior of the mice was noted. Some always remained under the igloo until it was raised and then immediately jumped across to the other rod. Others spent little time in the igloo and explored the platform freely between jumps. Much urging was necessary before most of the mice would jump the greater distances, although a few jumped them without being impelled by the raising of the igloo. While there was a certain amount of variability in the behavior of any one mouse from time to time, it was less than between any two individuals tested.

In jumping the mice seemed to depend not only upon vision but also upon an awareness of the degree of success achieved in the previous jump. When a mouse had barely succeeded in jumping a certain distance, it generally expended a little more effort in the next jump, whereas a mouse which had greatly overjumped expended less effort. That the mice sometimes seemed to judge distances more by kinaesthetic cues from the previous jump than by visual cues was indicated by the overjumping of certain mice when the rods had been moved closer together immediately following a successful jump. The exact nature of the interplay between visual, kinaesthetic, and other cues was not determined. It can only be stated here that both the visual and kinaesthetic seemed to be of importance in guiding the jumping of the mice from rod to rod. It is possible, too, that echolocation (Griffin, 1944) may have been employed by the mice.

During the jump the forefeet were extended forward. The hind legs, extended somewhat posteriorly immediately following the take-off, were gradually pulled forward under the body as the animal approached the second rod. The movements of the appendages were similar to those illustrated in Plate II, B-K. Usually, the tail was carried straight behind or slightly upward, but was sometimes moved markedly up at the very beginning of the jump. The tail appeared to be of great importance in helping the mouse balance itself on the landing rod. The mice jumped straight forward from one rod to the other, and there was no indication that the tail was used as a rudder to direct the course. All jumps were made from a standing or crouching position on the starting rod and were, therefore, of the type known as the standing broad jump.

Fourteen mice were tested. Ten of them were one-year-old females, one representative of each form. The others were four littermate gracilis, two males and two females, two months old.

The maximum jumps made by the 10 year-old females (Table IX) ranged from 39.0 to 66.5 cm. The greatest jumps were executed by three of the semiarboreal individuals and the shortest by the four terrestrial. Intermediate jumps were exhibited by the semiarboreal oreas and gracilis and by rubidus. The average maximum jump (57.0 cm.) of the five semiarboreal mice is considerably greater than that (42.0 cm.) of the four terrestrial mice. The ratios of maximum jump to body length (Table IX) show that the distances jumped by the mice ranged from 4.47 to 6.79 times the body lengths of the individual mice. In general, the distances attained by members of the semiarboreal forms were relatively greater than those attained by the terrestrial, although there was some overlapping in relative performance.

The maximum jumps made by the four two-month-old gracilis (Table X) ranged from 48.0 to 53.0 cm. The average jump (51.3 cm.) of these mice differed only slightly from the jump (49.5 cm.) of the gracilis in the group of one-year-olds. There was no marked difference in the performance of the two sexes in the two-month-old gracilis group; the two females exceeded by only 2.5 cm. the average jump made by the two males. The ratios of maximum jump to body length among the four young gracilis are more variable than their absolute jumping distances. Such consider-

TABLE IX

Maximum Jumping Performance of Ten Peromyscus

Standing broad jump. One-year-old females.

Species and Subspecies	Maximum Distance Jumped (cm)	Ratio of Maximum Jump to Body Length
maniculatus bairdi	39.0	4.76
maniculatus blandus	42.5	4.47
polionotus leucocephalus	42.5	5.25
maniculatus nebrascensis	44.0	4.54
maniculatus oreas	48.0	5.05
maniculatus rubidus	48.5	5.22
maniculatus gracilis	49.5	5.38
leucopus noveboracensis	60.0	6.45
nasutus nasutus	61.0	6.29
truei truei	66.5	6.79

able variability in this ratio among littermates suggests that it is less valuable as a measurement of jumping ability than the more uniform absolute jumping distance. It is worthy of note here that the four younger gracilis individuals were as proficient in jumping as the one-year-old, because under natural conditions two-month-old mice are entirely dependent on their own abilities to escape from predators and jumping proficiency could be of great usefulness to them when pursued.

The results of the experiment on jumping may be summarized as follows. Mice of all of the forms could be trained to jump horizontally from one rod to another through distances at least four times as great as their respective body lengths. In general, the maximum performance

TABLE X

Maximum Jumping Performance
of Four Peromyscus maniculatus gracilis Littermates

Standing broad jump. Two-month-old males and females.

Sex	Maximum Distance Jumped (cm)	Ratio of Maximum Jump to Body Length
Male	48.0	5.58
Female	52.5	6.03
Male	53.0	5.89
Female	53.0	6.39

of mice of the semiarboreal forms tested exceeded that of the terrestrial, both in actual distance jumped and in ratio of jumping distance to body length. Four two-month-old gracilis showed only slight individual differences in jumping ability and none of them differed markedly in ability from a single one-year-old gracilis. Although spontaneous jumping from branch to branch under natural conditions may be infrequent, it is nevertheless significant that, when forced to jump, semiarboreal mice can jump farther than the terrestrial mice.

V. Climbing on Small Branches

In peromyscus proficiency in climbing along small branches varies with the nature of the branch. The characteristics of a branch which most influence proficiency are hardness of surface, inclination, flexibility, accessibility of nearby branches, roughness of surface, and diameter.

1. Hardness of Surface. -- Because of the difficulty in maintaining surfaces of a given hardness at a uniform degree of roughness throughout a test period, no measurements were made of the proficiency with which the mice traveled along branches of various degrees of hardness. Nevertheless, it was evident that very hard surfaces greatly restricted the use of the claws of the mice. Hard surfaces impeded progress less on smaller branches which could be grasped readily by the digits than on those of larger diameter. Hardness was also of less hindrance to the mice when the branches were very rough.

2. Inclination. -- Branches which sloped upward at a given angle were more easily traveled than were like branches which sloped downward at the same angle from the horizontal. The mice always ascended and descended the sloping branches head first. The tail was sometimes flexed about an acclivous branch (Pl. VI, N) and occasionally used as a brace to prevent the mouse from slipping backward, but flexing of the tail about declivous branches, to keep the mouse from sliding forward, was more frequent. A flexed tail is capable of exerting considerable pressure on a branch, thereby acting as a brake. This use of the tail as a brake is illustrated in Plate VI, O, where a mouse is descending a freely hanging sash cord. The pressure of the tail against the cord is sufficient to cause a slight bending of the cord. Whenever a mouse slipped to the underside of a branch, either during ascent or descent, the tail was flexed over that branch to help support the suspended body of the animal (Pls. III, D-E; IV, G).

3. Flexibility. -- Observations of the locomotion of the mice, whether along artificial branches of baling wire covered with adhesive tape, natural branches denuded of twigs, or tape-covered fly rods, showed that all of them experienced a progressively greater difficulty in staying upright which was in rough proportion to the flexibility of the branch. In general, the heavier the animal and the greater its speed, the more the branch swayed; the greater the induced sway, the greater the difficulty of the mouse in maintaining its balance; and the more difficult it was for

the mouse to remain upright, the more the tail was used to help maintain that position.

In measuring the comparative abilities of the mice to travel upright along flexible branches, three adhesive-tape-covered fly rods of progressively increasing flexibility were employed. Each slightly tapered rod was approximately 2 1/2 feet in length and 5 mm. in diameter. Each rod was firmly attached at its larger end to an elevated platform upon which was placed an igloo with a sunflower seed within it. The free end of each rod was adjacent to another elevated platform also provided with an igloo and sunflower seed. Once the mice had been trained to proceed from platform to platform by crossing laths and roughened glass tubes, they were offered the flexible fly rods as pathways from one platform to the other.

Twenty mice were tested, one of each sex from each form. Each mouse was scored during its initial progression along the length of each of the three flexible rods and the scores recorded in terms of errors rather than of achievement as follows:

0 errors. Mouse progressed from attached end of rod to support at free end of rod without losing its balance.

1 error. Mouse fumbled once but regained its foothold. A fumble involved loss of footing of only one foot (almost always a hind foot), the body of the mouse remaining all the while above, or chiefly above, the rod. Fumbling movements are illustrated in Plate IV, B-D.

2 errors. Mouse fumbled two or more times, each time recovering its foothold.

3 errors. Mouse regained its upright position after slipping into a position wherein its body fell below the rod (Pl. IV, F-L).

4 errors. Mouse slipped two or more times but regained its normal position each time.

5 errors. Mouse slipped and did not regain its upright position. Of the mice which made five errors, some fell to the ground, some dropped to the ground, and some completed the crossing by pulling themselves across the rod in an upside-down position.

In crossing a rod the mouse was given a score corresponding to its maximum error rating. Thus, a mouse which first fumbled but later slipped was given a score of 3 points; a mouse which recovered from 3 slips and then fell to the ground on the fourth slip was given a score of 5 points. Since 3 rods were included in each test, the maximum score which any mouse could make was 15 points. The minimum score of 0 indicated that there was no loss of balance on any of the 3 rods. That the mice experienced progressively greater difficulty in traveling along rods of increasing flexibility is evident from their total scores. The 20 mice made a total of 81 errors. Of this total, 9 errors were made on the least flexible, 30 on the more flexible, and 42 on the most flexible of the rods.

Average scores for the two individuals of each form tested are listed in Table XI, together with the average body weights and tail lengths of these same individuals. Since no marked sexual differences were revealed by the measurements, the sexes have not been considered separately. The scores show, as did extensive observations, that noveboracensis was best able to maintain its balance on the flexible rods (average score, 0.0) and blandus least able (average score, 12.5). Between these two extremes the individuals of the terrestrial forms nebrascensis, leucocephalus, and bairdi made fewer errors than some and more errors than others of the semiarboreal mice. The average score made by the semiarboreal mice, as a group, was 3.6 errors; while the average score of the terrestrial mice, as a group, was 5.6. This difference in performance between the two groups is not of statistical significance (t equals 1.06).

TABLE XI

Mean Errors in Locomotion by Peromyscus on Flexible Fly Rods
and Mean Weights and Tail Lengths of Individuals Tested

Sexes not separated. Weight recorded to nearest gram;
tail length, to nearest millimeter.

Species and Subspecies	Number of Mice Tested	Mean Number of Errors	Mean Weight	Mean Tail Length
Terrestrial:				
maniculatus bairdi	2	2.0	16	71
maniculatus blandus	2	12.5	20	67
maniculatus nebrascensis	2	5.0	17	64
polionotus leucocephalus . .	2	3.0	15	59
Intermediate:				
maniculatus rubidus	2	5.5	25	95
Semiarboreal:				
maniculatus gracilis......	2	3.5	19	96
maniculatus oreas........	2	1.5	21	116
leucopus noveboracensis . .	2	0.0	22	99
nasutus nasutus	2	8.5	29	107
truei truei...............	2	4.5	24	94

Except for blandus, mice of all of the terrestrial forms averaged lighter in weight than any of the semiarboreal. The difference in weight between the ten semiarboreal individuals, as a group, and the eight terrestrial individuals, as a group, is highly significant (t equals 3.44). The effect of heavier body weight on increasing the sway of branches and the difficulty of maintenance of balance has been mentioned. It is interesting, therefore, that the semiarboreal group, despite its significantly greater weight, made fewer errors in progression along the fly rods than did the terrestrial group.

The amount of swaying of a branch is affected not only by the weight of the mouse, but also by the speed of progression of the mouse along it. Rapidly moving mice propel their weights forward more forcefully than do slowly moving mice, thus producing a greater and more rapid bending of the branch. Since the mice which traveled most rapidly were usually the ones which made the fewest errors (only the semiarboreal noveboracensis and oreas traveled noticeably faster than the others), rate of progression alone is not an important factor in accounting for the relatively large number of errors made by the terrestrial mice.

In hind-foot length, the mean for the semiarboreal individuals was significantly greater than the mean for the terrestrial (t equals 5.95), but the ratio of hind-foot length to body length averaged the same (0.23) in both groups of mice. Moreover, the ratio which seems to be of even greater importance in the present experiment, that of foot length to body weight, actually was greater in the terrestrial group (1.14) than in the semiarboreal (0.98). It is doubtful, therefore, whether the absolutely greater foot length of the semiarboreal individuals gave them any advantage over the terrestrial individuals in this experiment.

A factor, in addition to body weight, which appeared to be of major importance in affecting maintenance of balance during progression along the flexible rods was tail length. The greater efficiency of the longer tail in the maintenance of balance was observed throughout. Not only could the tip of the longer tail circumscribe a greater arc, without involving the base of the tail to the extent of seriously dislodging the hind quarters, but a shift in balance which required circumscription of a large arc by a short tail required a much slighter movement by a long tail. The semiarboreal mice have markedly longer tails (Table XI) than the terrestrial mice and this difference in tail length between the two groups is highly significant (t equals 9.25). The longer tail of the semiarboreal forms seems, then, of primary importance in enabling these generally heavier animals to progress more proficiently than the lighter, shorter-tailed terrestrial ones. The difference in tail length between the two groups was sufficient, apparently, to more than compensate in performance for the greater swaying occasioned by the heavier semiarboreal mice.

Tail length in the semiarboreal group was not only absolutely longer than in the terrestrial group, but relatively longer in proportion to body length and to body weight. The ratio of tail length to body length averaged 1.07 in the semiarboreal individuals and 0.76 in the terrestrial individuals; that of tail length to body weight averaged 4.50 in the semiarboreal and 3.83 in the terrestrial. Although observations of the progression along flexible branches of mice differing appreciably only in ratio of tail length to either body length or body weight were few, the advantage in demonstrated ability seemed almost always to be possessed by the mice with the relatively longer tails. It seems probable, therefore, that in the progression of mice along flexible branches the longer tail is of greater value than the shorter not only because of its absolutely greater length, but also because of its greater length in proportion to both body length and body weight.

Several conclusions may be derived from these observations and measurements concerning the proficiency of the mice in traveling along flexible branches. Proficient locomotion of peromyscus on branches becomes progressively more difficult as the flexibility of the branch increases. Increasingly greater sway of a branch renders more difficult the maintenance of balance by the mouse. In progressing along a small flexible branch a heavy mouse produces a greater swaying than does a lighter mouse. The tail is used as a balancing organ in maintaining upright progression along a branch. In general, the long tails of the semiarboreal mice proved more effective as balancing organs than did the shorter tails of the terrestrial mice.

4. Accessibility of Nearby Branches. -- The progression of a mouse was frequently aided, when other branches were within reach, by pressing the tail against, or flexing it over, an accessible branch (Pl. VII, U-X). The mouse became aware of the exact position of such branches and their degree of flexibility by exploratory tail movements. The more twigs or branches that were accessible and the less flexible they were, the greater the use the mouse could make of them. The mouse availed itself of branches within reach usually only when progression became somewhat difficult. At these times greater movements of the tail increased the likelihood that it would come into contact with accessible branches.

In one experiment in which mice were required to descend a steeply inclined flexible branch bearing laterally projecting twigs, members of all 10 forms relied heavily upon flexing their tails over the twigs during descent. The tails were sometimes looped over the twigs at some distance from the branch, but were more commonly flexed over the twigs at their regions of insertion on the branch. Instances of looping the tail over a twig and then under an adjacent branch were also frequent.

In another experiment the mice were forced to cross horizontal tubes of progressively lesser degrees of both roughness and diameter. Paralleling each tube, above and to the side, was a taut wire. All of the mice used the wire when it was sufficiently close to them to be reached by their tails and when progression was sufficiently difficult to make the wire useful. Often, flexing the tail over the wire prevented a mouse from losing its balance. Lateral deviation of the hind quarters of the body came to an abrupt halt as the tail quickly tightened on the wire. Often a mouse held its tail so close to the wire during difficult progression that flexing over the wire or bracing against it was almost immediate when loss of balance seemed imminent. Not only was the wire used during unsteady progression, but it was used also to assist the animal in righting itself once it had slipped under the tube; the animal either pushed against or pulled on the wire with its tail in regaining an upright position. Although mice of all of the forms made use of the wire, when it was within reach of their tails, placement of the wire as far as 2 1/2 inches from the tube gave the longer-tailed semiarboreal individuals a tremendous advantage over the shorter-tailed terrestrial ones.

5. Roughness of Surface and Diameter. -- Decreased roughness of surface and decreased diameter of branch were both associated with greater difficulty of progression. The two factors are considered together,

not because they are more closely related than are any of the other variable characteristics of branches, but for convenience in describing the following experiment.

This experiment was designed to measure the comparative abilities of peromyscus of the several forms to maintain their balance on branches of relatively small diameter and relative smoothness. Artificial branches consisting of glass tubes which differed only in roughness, diameter, or both, were used. The sizes and roughnesses of the tubes chosen, on the basis of preliminary experiment, were those best suited to demonstrate the diverse abilities of individual mice to travel along hard-surfaced, nonflexible, twigless, horizontal branches. The tubes selected were not only sufficiently easy to cross that the majority of the mice could be trained to cross them upright, but sufficiently difficult that differences in crossing ability were apparent.

The apparatus consisted of two elevated platforms connected by the stick or tube to be crossed (Pl. I, C). Each platform, 14 inches in diameter and 27 inches in height, was supported from below by a metal rod. At the center of each platform was an igloo and within it a sunflower seed. The effective length of each tube was 22 inches and any tube was readily replaceable by any other. Six tubes, two each of three progressively lesser diameters and two degrees of roughness, were employed. The combinations and order in which they were presented are tabulated below.

Outside Diameter (mm.)	Crystolon Covering (mesh)
7	220
7	600
5	220
5	600
3	220
3	600

The tube-crossing tests were conducted under dim light in one of the compartments of the large experimental room. In the ceiling fixture of this compartment was a single 10-watt bulb and in that of the adjacent compartment a 15-watt. Each mouse was so placed on the platform that it could travel directly into the igloo. After a two-minute orientation period the igloo was slowly raised and the animal exposed on the platform. Usually the mouse soon crossed the 1-inch-broad stick leading from the first to the second platform and went into the second igloo. The first igloo was then lowered, a one-half-inch-broad stick substituted for the 1-inch stick, and the second igloo raised. Generally, the mouse went almost immediately to the stick and traveled back to the first platform. The igloo was lowered on the second platform, the first tube in the series substituted for the second stick, and the first igloo was again raised. This procedure was repeated until each of the six tubes had been crossed twice in succession by the mouse. Always the observer stood behind the igloo while raising it, with the doorway of the igloo facing the tube to be crossed. The sunflower seed was replaced whenever it had been eaten.

The method of scoring the tube crossings was the same as that used in scoring the flexible-fly-rod crossings (see 3, above); the scores, as there, were recorded in terms of total errors. The stick crossings, used to familiarize the animals with the apparatus, were not scored. Since each of the six tubes was crossed twice, there was a total of 12 scored crossings per mouse. The daily score of any mouse, therefore, could range from 0 points, for no loss of balance on any of the crossings, to 60 points, for irretrievable loss of balance on each of the crossings. The actual range of the daily scores was 0 to 45.

Preliminary experiments revealed considerably more day-to-day variability in performance than could be attributed to improvement due to training. Inasmuch as preliminary experiments had shown that the mice of the several forms responded similarly to training, it was believed that a mean score based on several daily tests might give a more valid measurement of the proficiency of a mouse than one based on a single test. The mean score of five successive daily tests, therefore, was decided upon as a measure of proficiency for each mouse. This particular number of tests was chosen because: (a) at the end of five tests none of the forms of mice had reached maximum tube-crossing proficiency and, since actual maximum proficiency for some forms was beyond the limit to be tested, the most proficient mice were thus placed at less disadvantage from a comparative standpoint than if more tests were used in calculating the mean; and (b) the use of five successive tests gave a mean which diminished the effect of day-to-day variability in performance and which was not, at the same time, influenced appreciably by effects on motivation as sometimes resulted from excessive training.

Eighty-one mice were tested. They included at least four individuals of each of the forms except rubidus. Of rubidus there was only one representative. Males and females were approximately equal in number. The age range was 13 to 109 weeks. Since neither sex nor age was associated significantly with differences in performance, results are presented as a single figure for each kind of mouse.

Just as the tube-crossing proficiency of any individual was represented by the mean of the number of errors made in five successive daily tests, so that of any form was represented by the mean of the mean daily scores of the several individuals of that form tested. The performance means for the forms, with the standard errors, are listed in Table XII. The data there show that each of the terrestrial forms averaged a greater number of errors than did any of the semiarboreal. In addition, the means of all of the semiarboreal forms, except nasutus, differ significantly from the means of all of the terrestrial forms. The mean of nasutus differs significantly only from those of nebrascensis (difference equals 7.6 errors; t equals 2.13) and noveboracensis (difference equals 5.5 errors; t equals 2.70). The score of the single rubidus was within the range of the semiarboreal rather than the terrestrial means.

The effect of training on improvement in performance was marked.

Of the total of 4939 errors made by the 81 mice in the course of the experiment, 1605 errors (32.5 per cent) were made the first day; 1023 (20.7 per cent) the second day; 864 (17.5 per cent) the third day; 778 (15.8 per cent) the fourth day; and 669 (13.5 per cent) the fifth day. Improvement was most pronounced immediately following the first test; the rate became more gradual thereafter.

TABLE XII

Tube-crossing Proficiency of the Several Forms of Peromyscus as Measured by Mean Errors Made in Crossing Selected Tubes during Five Successive Tests

Performance means and standard errors of individual means.

Species and Subspecies	Number of Mice Tested	Mean Errors in Performance
Terrestrial:		
maniculatus bairdi	8	15.2 ± 2.39
maniculatus blandus	6	19.5 ± 3.74
maniculatus nebrascensis	12	18.8 ± 1.93
polionotus leucocephalus	14	15.0 ± 1.35
Intermediate:		
maniculatus rubidus	1	9.0
Semiarboreal:		
maniculatus gracilis	21	6.9 ± 0.66
maniculatus oreas	6	9.1 ± 1.10
leucopus noveboracensis	4	5.7 ± 0.73
nasutus nasutus	4	11.2 ± 1.87
truei truei	5	7.3 ± 1.40

The total errors for each form are presented in Table XIII. In this table the totals for the second day have been combined with those for the third day and the totals for the fourth day with those of the fifth day. The distribution of errors shows that the various subspecies conform fairly well to the pattern of improvement cited above for the 81 mice as a group. The percentage of total errors made on the first day was, in general, considerably higher than that made on the second and third days and still higher than that made on the fourth and fifth days.

The arrangement of the data in Table XIII, in order of increasing percentage of total errors made during the first test, suggests, nevertheless, a difference in the rapidity of learning of the mice. The semiarboreal mice, on the whole, appear to have made more rapid improvement in tube-crossing proficiency than the terrestrial mice. The testing technique, however, was better adapted to more accurate measurement of the abilities of the terrestrial than of the semiarboreal forms. Since the most proficient mice could have crossed tubes of greater difficulty than those included in the experiment, such mice sustained a slight handicap and they might well be expected to make a larger percentage of their

TABLE XIII

Effect of Training on Tube-crossing Performance of Peromyscus, as Shown by Errors Made in Crossing Selected Tubes during Five Successive Tests

Species and Subspecies	Number of Mice Tested	First Test		Second and Third Tests (results combined)		Fourth and Fifth Tests (results combined)	
		Total Errors	Percentage of Errors	Total Errors	Percentage of Errors Per Test	Total Errors	Percentage of Errors Per Test
maniculatus blandus.......	6	169	28.9	237	20.3	178	15.2
maniculatus nebrascensis..	12	329	29.2	443	19.7	354	15.7
maniculatus oreas	6	83	30.3	121	22.1	70	12.8
maniculatus bairdi........	8	186	30.6	206	16.9	216	17.8
nasutus nasutus...........	4	71	31.8	96	26.5	56	12.6
maniculatus rubidus.......	1	15	33.3	20	22.2	10	11.1
polionotus leucocephalus...	14	364	34.5	400	19.0	289	13.7
maniculatus gracilis.......	21	262	35.9	263	18.0	204	14.0
leucopus noveboracensis...	4	45	39.5	35	15.4	34	14.9
truei truei	5	81	44.3	66	18.0	34	9.3
Total...............	81	1605	32.5	1887	19.1	1447	14.6

errors on the first day and a relatively smaller number on the succeeding days than would the less proficient mice. Consequently, that the scores of the semiarboreal forms improved more rapidly than did those of the terrestrial forms indicates, chiefly, greater arboreal ability rather than more rapid learning.

Factors other than the nature of the test undoubtedly affected the relative number of errors made by various individuals on successive test days. Among these may be noted certain differences in general behavior. For example, of all the mice tested several truei and leucocephalus showed the most marked difference in degree of excitement manifested during the first test and that exhibited during the last. A few which were greatly excited on the first test appeared very much at ease even on the second. This decrease in excitement may well account for their larger percentage of total errors made on the first day than might otherwise have been expected. The oreas mice, on the contrary, were noticeably calm even during the first test period. The first day they usually crossed the tubes directly, but on following days they tended to loiter along the tubes, often sitting there and washing their faces. In attempting to wash while sitting on a tube, they occasionally fumbled or slipped. Recovery was easy, and once an individual had slipped it behaved more cautiously thereafter. The relatively large number of errors made by oreas during the second and third tests is at least to some extent, therefore, a reflection of its general behavior. Furthermore, since oreas made many of its errors while loitering along the tubes, its performance mean somewhat underestimates its true tube-crossing ability.

From the foregoing discussion it seems evident that the data of Table XIII include no marked differences in learning ability among the several forms of mice tested. Although this experiment has not been designed to discover it, it is nevertheless possible that considerable individual and racial variability exists in peromyscus with regard to learning ability.

In the course of the experiment disqualification of certain individuals which were injured or did not adapt themselves to the experimental procedure became necessary. Of these mice, there were two which repeatedly jumped from part way across a tube to the opposite platform, one which persisted in somersaulting backward from the platform, and another which sustained a foot injury after the third day's test. Three mice which repeatedly dropped to the ground and five which repeatedly jumped were also eliminated. Elimination of certain individuals might be judged to affect the results of the experiment. But comparison of the incomplete scores of all the discarded mice with comparable parts of scores of mice of the same forms which had not been eliminated, showed remarkably slight differences in performance up to the time of disqualification.

Throughout the experiment environmental factors were controlled as carefully as practicable, and the mice were tested, in general, by the pairing technique. It seems unlikely, therefore, that whatever slight variability in environmental stimuli may have existed should have affected the mice of any one form more than another.

That decreased roughness and decreased diameter of small branches both limited the progression proficiency of peromyscus was a matter of common observation. Measurement of the effect on proficiency of the difference in roughness used was computed from the total errors that the 81 mice made in crossing the tubes of each roughness. Of the total errors (4939), 2059 (41.7 per cent) were made on the three tubes of greater roughness (220-mesh Crystolon covering) and 2880 (58.3 per cent) on the three of lesser roughness (600-mesh Crystolon covering). The smoother tubes are, therefore, shown to be more difficult to cross than the rougher ones. The conclusion is even more convincing in view of the fact that the smoother tube, at any given diameter, was in each case the second one crossed and the mice had thus had the benefit of previous experience.

Measurement of the effect on proficiency of the different diameters used was calculated from the total errors made by the 81 mice in crossing the tubes of each diameter. Of the 4939 errors, 344 (7.0 per cent) were made on the two tubes of 7-mm. diameter; 1003 (20.3 per cent) on the two of 5-mm.; and 3592 (72.7 per cent) on the two of 3-mm. Although the tubes were presented in order of decreasing diameter so that the mice had greater experience before crossing the smaller, the mice made an increasing percentage of errors as the diameter decreased. There can be no doubt that proficient locomotion along small branches must also become progressively more difficult as their diameters decrease, for differences in proficiency were marked with respect to a 2-mm. difference in diameter in the tubes employed.

In this experiment the tubes were made progressively more difficult to travel by combining decrease of roughness with decrease of diameter. The effect of this graded series of tubes in limiting the tube-crossing proficiency is to be seen from the total errors made by the mice on each of these tubes. Of the 4939 errors made by the 81 mice, 49 (1.0 per cent) were made on the first tube (7 mm. diameter, 220-mesh covering); 295 (6.0 per cent), on the second tube (7 mm. diameter, 600-mesh covering); 373 (7.6 per cent), on the third tube (5 mm. diameter, 220-mesh covering); 630 (12.8 per cent), on the fourth tube (5 mm. diameter, 600-mesh covering); 1637 (33.1 per cent), on the fifth tube (3 mm. diameter, 220-mesh covering); and 1955 (39.6 per cent), on the sixth tube (3 mm. diameter, 600-mesh covering).

The results of this tube-crossing experiment may be summarized briefly. The locomotion of peromyscus along small-diametered roughened tubes became more difficult with progressive decrease in diameter, progressive decrease in roughness, or both. The semiarboreal forms noveboracensis, gracilis, truei, and oreas were significantly more proficient in tube crossing than were the terrestrial forms leucocephalus, bairdi, nebrascensis, and blandus. Nasutus was more or less intermediate in proficiency, although its performance mean is closer in value to those of the other semiarboreal forms than to those of the terrestrial. The single rubidus individual was also closer to the semiarboreal in performance than to the terrestrial forms. With training, all of the mice of the several forms became more proficient, and there was little difference in the rate of improvement which could not be attributed either to difference in arboreal ability or to difference in general behavior. Since proficiency in the progression of peromyscus along small branches is undoubtedly of great importance under natural conditions, it is most significant that the mice of the semiarboreal forms proved better adapted for such locomotion than those of the terrestrial forms.

VI. Effect of Tail Amputation on Climbing Proficiency

The use of the tail in climbing was described above under Climbing Behavior. Observations and previous experiments had shown that tail length is positively correlated with climbing proficiency in the mice. The object of this experiment, therefore, was to measure the effectiveness of the tail as an aid to proficient locomotion along small branches. In progression along such branches the tail functions chiefly as a balancing organ or as a prehensile organ which assists in the recovery of an upright position by the mouse if slipping occurs. The apparatus and procedure followed were the same as those of the immediately preceding experiment.

In the main part of the experiment the mice were divided into an amputation group and a control group. The amputation group consisted of 10 gracilis, 10 nebrascensis, and 10 leucocephalus. Their tube-crossing proficiency was tested on five successive days. The tail of each mouse was then amputated. After a one-month period of convalescence, by which time the wound had healed over completely, the 30 mice were retested in the same manner on five successive days. The control group consisted of six gracilis, four nebrascensis, and two leucocephalus, all with normal tails. Except for not amputating their tails, the controls were treated exactly like the mice of the amputation group and two series of tests run on them. The sexes were equally divided for each form in both groups. The ages of the animals ranged from 14 to 68 weeks. Since neither age nor sex was significantly correlated with differences in performance, no distinction has been made in presenting the results (Table XIV).

In the first series of tests the mean number of performance errors made by each of the three forms of the amputation group (prior to amputation) was similar to that of the corresponding form in the control group. Moreover, the difference between the mean of the amputation group and that of the control group of the same form was less than that between means of different forms. In the second series of tests the mean score made by the control mice of each form was considerably lower in each case than that made during the first series. That the mean scores of the controls were lower than those made during the first series is to be attributed not only to greater proficiency resulting from learning which was carried over, but to a continuation of the learning throughout the second series. After amputation, the gracilis mice made significantly more errors than they had made with tails intact (difference equals 7.8 errors; t equals 4.22); the nebrascensis showed practically no difference in mean performance after amputation; and the leucocephalus attained a mean

TABLE XIV

Effect of Tail Amputation on Tube-crossing Proficiency
in Three Forms of Peromyscus

Performance means and standard errors of individual means.

Species and Subspecies	Number of Mice Tested	Mean Number of Errors in Performance		
		First Series of Tests	Second Series of Tests	
		Mice with Tails Intact	Mice with Tails Intact	Mice with Tails Amputated
maniculatus gracilis (amputation group)........	10	6.7 ± 1.07	....	14.5 ± 1.52
maniculatus gracilis (control group)...........	6	5.9 ± 0.60	2.6 ± 0.00	....
polionotus leucocephalus (amputation group)........	10	15.6 ± 1.63	....	13.1 ± 1.16
polionotus leucocephalus (control group)...........	4	13.7 ± 2.60	8.7 ± 1.32	....
maniculatus nebrascensis (amputation group)	10	18.2 ± 2.20	....	18.1 ± 1.70
maniculatus nebrascensis (control group)...........	2	20.3 ± 6.72	12.3 ± 5.52	....

score lower by 2.5 errors. This does not signify, of course, that nebrascensis and leucocephalus perform just as proficiently or more proficiently without tails as with them, but that the proficiency of nebrascensis and leucocephalus amputees was less affected by loss of the tail than was that of gracilis amputees. Although learning affected favorably the proficiency of all the mice, the amputees of the three forms averaged considerably more errors than did their racial relatives among the retested controls. It is quite evident, therefore, that removal of the tail did greatly handicap the mice in crossing the tubes.

As has just been noted, performance of the gracilis amputees was more affected by tail removal than was that of the other amputees. The gracilis controls made a significantly lower mean score on the second series of tests than on the first (difference equals 3.3 errors; t equals 4.76), whereas gracilis amputees made a significantly higher mean score than they had previously made with tails intact (difference equals 7.8 errors; t equals 4.22). Hence, taking the control group of gracilis as a standard, one would expect the gracilis amputees to make a mean performance score of approximately three points, if tail removal had no effect on their tube-crossing proficiency. But the actual mean score was 14.5 points, which indicates that the amputees presumably made four to five times more errors during the second tests than they would have had their tails not been removed. Similarly, it may be estimated that nebrascensis and leucocephalus made at least one and one-half and one and one-third times more errors, respectively, on the second series of tests than if they had still had their tails. These estimates offer further proof that, although tail removal reduced the tube-crossing proficiency of all three forms, gracilis suffered a far greater handicap than did either nebrascensis or leucocephalus.

The mean tail-length measurements, with the standard errors, for those individuals of the three forms which were included in the amputation group are listed in Table XV. Each tail-length mean differs very significantly from every other tail-length mean, the difference between the means of gracilis and nebrascensis being considerably greater (difference equals 31.40 mm.; t equals 15.91) than that between the means of nebrascensis and leucocephalus (difference equals 9.40 mm.; t equals 5.82). The mean length of the tail stub remaining after amputation varied only slightly and never significantly in the three forms. This virtually ineffective tail stub was in all instances so short as to be barely evident. Although amputees of the three forms were closely comparable in length of tail stub, they had originally been markedly different in length of tail.

A comparison of tail-length measurements with the estimated effects of tail removal on proficiency showed that the long tail of gracilis is a more effective aid in tube crossing than is the shorter tail of either of the other two forms. Furthermore, the tail of nebrascensis, which is somewhat longer than that of leucocephalus, is somewhat more effective than is the tail of that form. According to the performance means, the tube-crossing ability of leucocephalus was least affected by tail removal. The gracilis amputees attained a mean score more or less intermediate between the mean scores of the leucocephalus and the nebrascensis

TABLE XV

Means and Standard Errors for Body Measurements of Peromyscus of Amputation Group

Body dimensions recorded in millimeters; weight, in grams.

Species and Subspecies	Number of Mice Tested	Original Tail Length	Tail Length After Amputation	Body Length	Foot Length	Body Weight
maniculatus gracilis	10	96.10 ± 1.48	12.60 ± 0.92	95.70 ± 1.35	20.97 ± 0.29	21.7 ± 1.20
maniculatus nebrascensis......	10	64.70 ± 1.38	13.10 ± 0.72	88.20 ± 1.59	19.09 ± 0.16	18.5 ± 1.35
polionotus leucocephalus.......	10	55.30 ± 0.86	11.60 ± 0.45	78.40 ± 1.31	18.48 ± 0.15	14.5 ± 0.45

amputees, whereas before tail removal gracilis had a mean score significantly lower than that of either of them (difference equals 8.9 and 11.5 errors, respectively; t equals 4.54 and 4.71, respectively). On the other hand, the performance means of nebrascensis and leucocephalus differed more from one another after tail amputation (difference equals 5.0 error points) than before (difference equals 2.6 points). The longer tail of nebrascensis apparently compensated somewhat for certain other factors, as perhaps its greater weight, its relatively shorter hind foot, or both. The actual effects of other differences in body measurements on the tube-crossing proficiency of the mice cannot be assessed from the results, but the positive correlation of tail length with tube-crossing proficiency is marked.

As a part of this experiment the tube-crossing proficiency of several additional gracilis was determined. Four of these underwent whole-tail removal and four underwent half-tail removal. The mice were operated on approximately three months before they were tested, and at the time of testing ranged from 57 to 64 weeks in age. The sexes were equally divided in each group.

The performance means for the two additional groups of mice are given in Table XVI and, for comparison, the mean score attained by the 10 gracilis of the amputation group (prior to amputation) from Table XIV. In body measurements the mice of these three groups differed significantly only in tail length (see mean measurements, Table XVI). Comparison of performance means and tail-length means shows clearly the dependence of tube-crossing proficiency on tail length. The normal animals showed considerably greater proficiency than the half-tailed ones and the half-tailed more than the virtually tailless. The data given in the two tables show that the 10 tailless gracilis had a score (14.5 ± 1.52) during the second series of tests (Table XIV) more or less intermediate between that of the half-tailed mice (11.7 ± 1.78) and that of the no-tailed mice (21.0 ± 3.31), during their one and only series of tests (Table XVI). Therefore, given mice of comparable tail length, then those with the greater amount of training demonstrate the greater tube-crossing proficiency; whereas in mice with equal amount of training, proficiency is more or less dependent on a longer or shorter tail.

All of the previously described operations had been performed on animals which were at least six months old, so that at the time of the operation the animals had already learned to climb about in their cages with their tails intact. None of the mice, however, had received any previous training in climbing outside of their cages prior to the tube-crossing experiment. It seemed possible that mice which had never known the assistance of a tail might learn to climb as proficiently without their tails as did those animals which had always had them. The following experiment was carried out to ascertain whether mice which had never learned to use tails could perform as well as those which had become dependent upon the presence of a tail. Two litters of gracilis were employed. In the first litter of four mice, one male and one female were deprived of their tails at the age of 10 days, and one male and one female were left with tails intact. In the second litter, one

TABLE XVI

Effect of Tail Amputation on Tube-crossing Proficiency in Several Groups of Peromyscus maniculatus gracilis

Performance means and standard errors of individual means.

Class	Number of Mice Tested	Mean Tail Length (mm.)	Mean Number of Performance Errors		
			Mice with Tails Intact	Mice with Half Tails	Mice with No Tails
Mice of amputation group (Table XIV)................	10	96.10 ± 1.48	6.7 ± 1.07	....	....
Mice more than six months old at time of operation	4	54.00 ± 1.36	....	11.7 ± 1.78	....
Mice more than six months old at time of operation	4	15.50 ± 1.45	....	....	21.0 ± 3.31
Mice ten days old at time of operation..................	4	14.00 ± 1.42	....	....	14.0 ± 2.34
Unoperated littermate controls	3	93.67 ± 3.67	6.7 ± 1.39	....	....

male and one female underwent the same operation 10 days after birth, and the remaining one, a female, was kept as a control. (At the age of 10 days the mice are still unable to progress in an upright manner.) When these mice were three months old they were each given five successive daily tests in tube crossing. The performance means for these animals are listed in Table XVI. The mean of 6.7 ± 1.39 errors made by the three control mice of the two litters is closely comparable to that (6.7 ± 1.07) made by the 10 gracilis mice when tested with their tails entire. A mean score of 14.0 ± 2.34 errors was made by the four mice which had never experienced the assistance of the tail in locomotion. A difference between the means of the four tailless mice and the controls of 7.3 points indicates that the tube-crossing proficiency of the long-tailed gracilis was not due alone to learned dependence upon the tail, although this difference falls just short of significance (t equals 2.43; $N_1 + N_2$ equals 7). However, the difference between the mean score of 14.0 ± 2.34 made by the mice early deprived of their tails and that of 21.0 ± 3.31 made by the four which had already learned to use the tail as an aid to locomotion (difference equals 7.0 points; t equals 1.74) suggests, but does not prove, that some learned dependence upon the tail was involved.

Since learned dependence upon the tail appears to be involved, it is advisable to apply a correction factor to the previously stated estimates of tail-length effectiveness. A 50 per cent reduction of the difference between the scores made by gracilis individuals before and after amputation would certainly be more than adequate, on the basis of the scores made by the mice which had never learned to use their tails, to compensate for the learned dependence of a long-tailed mouse upon its tail. It is well within the realm of conservatism, therefore, to conclude that gracilis individuals, when deprived of their tails, make at least twice as many errors, exclusive of those presumed to be due to learned dependence upon the tail, in progression along the described tubes as might be expected if their tails were intact. Although there is no basis for determining the reduction factor needed to compensate for learned dependence on the tail in either nebrascensis or leucocephalus, certainly neither of these forms would be expected to exceed the previously stated estimates of tail efficiency. There can remain no doubt, therefore, that the long tail of gracilis is a more effective aid to progression along small tubes, simulating small branches, than is the shorter tail of either nebrascensis or leucocephalus.

In conclusion, differences in the performance of three forms of mice before and after tail amputation demonstrated that the tail was of great importance as an aid to proficient progression along artificial branches of small diameter and relative smoothness of surface. The long-tailed, semiarboreal form gracilis suffered a greater reduction in proficiency, after the tail was removed, than did either of the shorter-tailed, terrestrial forms nebrascensis and leucocephalus. Furthermore, individuals of gracilis which underwent whole-tail removal suffered a greater loss in proficiency than did those which underwent half-tail removal. It was estimated that, when deprived of their long tails, gracilis would make at least twice as many errors in tube crossing as would be expected if their tails were intact and also that, when deprived of their shorter tails, nebrascensis and leucocephalus would make no more than one and one-half times as many errors as would be expected if their tails were intact. Hence, although in all three forms the tail is of adaptive value in locomotion along small branches, the long tail of the semiarboreal gracilis is of greater adaptive value than is the shorter tail of either of the two terrestrial forms tested.

DISCUSSION

Within the genus Peromyscus certain forms are restricted fairly closely to semiarboreal habitats, while others are limited more or less strictly to terrestrial habitats. In general, the forms which live in the wooded areas have tails which are longer than those of the forms which occupy open types of habitat. The semiarboreal forms studied in this investigation were gracilis, oreas, noveboracensis, nasutus, and truei; the terrestrial, bairdi, blandus, nebrascensis, and leucocephalus. An additional form, rubidus, was represented by a stock derived from animals inhabiting an extensive area of brushland near Hood River, Oregon, a type of habitat which is somewhat intermediate between wooded and open country. Despite the general paucity of literature concerning the behavior of these forms under natural conditions, it was concluded that the terms "semiarboreal" and "terrestrial" could properly be applied to the habits as well as to the habitats of the forms so designated. It is not known whether the behavior of the Hood River rubidus in nature resembles more closely that of the semiarboreal or that of the terrestrial mice. Since the rubidus mice are more or less intermediate with respect to habitat, however, it was presumed that they are more or less intermediate in climbing behavior.

The measurements of the mice (Tables V and VII) show that in all of the terrestrial forms the tails were not only absolutely but also relatively, when compared with body length, shorter than in those of the forms known to be somewhat arboreal in habit. The tail length of the Hood River rubidus stock was closer to that of the semiarboreal than to that of the terrestrial forms. Absolute tail length of the rubidus was exceeded somewhat by that of all of the semiarboreal forms with the possible exception of truei (Table VII), and the relative tail length was surpassed by all of the semiarboreal forms except possibly truei and noveboracensis.

Structural modifications, if they are to be of maximum effectiveness in nature, must be accompanied by appropriate reactions and, as has been shown in this study, the arboreal adaptations of peromyscus involve modifications not only of body structure but of general behavior as well. In the absence of pathways to the ground the semiarboreal forms showed a greater tendency to remain for a given length of time on an elevated platform than did the terrestrial forms. Rubidus, which inhabits a transitional type of habitat, was more or less intermediate between the two groups in its response to elevation. Most of the semiarboreal individuals which failed to remain at the elevated level seemed to leave that position intentionally and gave evidence of awareness of their general position above ground. On the other hand, most of the terrestrial individuals which failed to remain aloft appeared to leave the elevated position accidentally and to show less awareness of the general relationship of the support to the ground. The semiarboreal mice seemed also to be more at ease on elevated apparatus and less anxious, when pathways to the ground were available, to progress immediately downward. The semiarboreal peromyscus, then, by virtue of their greater tendency to remain at elevated levels, their greater awareness of the elevation, and their greater ease in climbing about on elevated apparatus, exhibit behavior which is more appropriate to scansorial habits than is that of terrestrial forms.

The types of progression which may be employed by peromyscus under natural conditions fall into three general categories: vertical climbing, progression from one to another of two noncontiguous branches, and progression along branches. In each category the tail is useful to the progression of both the terrestrial and semiarboreal forms, but in each type of progression the semiarboreal forms are more proficient than the terrestrial. In mice of all the ten forms the tail was occasionally used as a prop during vertical ascent. In descent, it was often pressed closely against tree trunks, or tubes, and employed as a brake. During descent the degree of rotation of the hind limbs in all of the forms was somewhat less than that commonly observed in the arboreal squirrels.

Each of the five semiarboreal forms of peromyscus was able to climb a significantly greater proportion of a series of roughened vertical tubes of various sizes and roughnesses than was any of the four terrestrial forms (Tables V - VIII). Some natural, as well as simulated, vegetation proved particularly difficult for individuals of the terrestrial forms to climb. Certainly, the semiarboreal mice are able to climb effectively a great number of the available trees and shrubs of most habitats, a factor of primary importance in the use of these types of vegetation for food, nesting sites, and escape from predators. Therefore, there can be no doubt that the semiarboreal forms, since less restricted in their ability to use available vegetation, are less handicapped in climbing vertically under natural conditions than are the terrestrial forms.

In progressing from one to another of noncontiguous branches a peromyscus tends to be very cautious. When the two branches are close together the animals "whisker" the second branch carefully and then extend one foot forward to that branch. If the second branch yields very little under the extended foot, the crossing is usually completed. In no instance was the horizontal reach from branch to branch greater than the body length of the mouse concerned. But in reaching directly downward from one to another of two artificial inflexible branches, several mice were able to span gaps which slightly exceeded their respective body lengths, for the animals were able to hang by their hind feet and tails while reaching toward the lower branch. Here the tail appeared to be of considerable importance as an aid to supporting the weight of any mouse as it hung downward. By means of its gradually diminishing hold on the upper branch following release of the hind feet from that branch, the tail also retarded the rate of dropping of the hind quarters of the animal and thereby facilitated accurate placement of the hind feet on the lower branch. That the long-tailed forms were able to span greater downward distances, in comparison to body length, than were the short-tailed forms further indicates that the tail is an effective aid to this type of gap spanning. In maximum upward reach the mice, by standing on their hind feet as they reached upward, were able to negotiate distances which were slightly greater than their respective body lengths. Reaching was preceded by markedly cautious exploratory behavior in all instances in which a mouse progressed for the first time from one small branch to another and the gap between the branches was more than approximately one-half its body length.

Although mice of all of the forms could be trained to jump distances greater than four times their respective body lengths in traveling from one to another of two small supports placed at the same distance above ground, it is questionable whether spontaneous jumping from branch to branch plays an important role in the usual locomotion of peromyscus. Spontaneous jumping from support to support in the laboratory was observed in only a few instances despite ample opportunity. Moreover, since effective jumping in nature would presuppose the ability to locate precisely a second support, the question arises as to whether these chiefly nocturnal animals are able to see their targets clearly or whether they have to rely on special accessory sensory mechanisms comparable perhaps to those employed by bats. Possibly, jumping from branch to branch is resorted to in nature only in times of emergency. McCabe and Blanchard (1950), however, in their report of extensive field and laboratory observation of P. maniculatus gambeli, P. californicus californicus, and P. truei gilberti, stated that brilliant climbing and jumping distinguish gilberti from the other two forms. Hence, it is perhaps of significance that the most frequent and spectacular of the jumps that were recorded here were those of P. truei truei, which is closely allied to P. truei gilberti.

That certain mice of this genus may fall great distances without suffering any apparent injury was noted by both Cahalane (1939: 434) and Hamilton (1928: 65-66). Cahalane witnessed the falling of a specimen of Peromyscus boyli rowleyi from an oak limb 20 feet above ground. The mouse held its legs out stiffly while falling, landed upright, and immediately ran away. Hamilton noted several instances in which noveboracensis mice leaped, when pursued, from the fourth floor of a building to the pavement below. None of the recaptured mice showed any evidence of injury, and "one large female gave birth to four normal young two days after such a fall" (Hamilton, 1928: 66). Similar records of falling from considerable distances without apparent injury have been described for the common house rat and the red squirrel (Hamilton, 1928: 66), as well as for the fox squirrel (Allen, 1943: 220).

The rate of frequency of injury as a result of falling is a factor of considerable importance to animals of scansorial habits, although not all climbing mammals seem so well adapted to falling as do those described above. Of the three forms of peromyscus studied by McCabe and

Blanchard (1950: 94), maniculatus gambeli and truei gilberti can be dropped considerable distances without ill effect, whereas californicus californicus, an efficient climber, "is likely to bounce off intervening branches and often lands unrighted with a heavy and in one instance deadly impact." Carpenter's field study of the gibbon, an animal which is far heavier than any of the above-mentioned rodents, indicates that a high percentage of the captured gibbons showed healed bone fractures (Carpenter, 1940: 70). Carpenter believed these injuries to have resulted from falls, particularly from falls in which weak branches break beneath the weight of the animals.

In progressing horizontally along roughened tubes simulating small branches all of the semiarboreal forms of peromyscus demonstrated greater proficiency than the terrestrial, and a large part of this was owing to the greater length of the tail. Differences in performance of mice of three forms, before and after tail amputation, showed that the long-tailed, semiarboreal gracilis suffered a greater handicap, as a result of unlearned dependence on tail use, than that sustained by the terrestrial forms, nebrascensis and leucocephalus, which are shorter tailed. Gracilis amputees made at least twice as many errors in tube crossing as would be expected had their tails been intact, whereas nebrascensis and leucocephalus amputees made no more than one and one-half the expected number of errors. The longer tail of gracilis is, therefore, of greater value as an aid to progression along small tubes and branches than is the shorter tail of the terrestrial forms. Experimental results showed also that the long-tailed, semiarboreal forms, as a group, exhibited greater proficiency in traveling along flexible artificial branches of small diameters, even though their greater average body weight produced a greater swaying of the branches. The length of tail of the semiarboreal forms was sufficient to more than compensate for the greater swaying of the branches effected by the greater weight.

Although long tails were more effective aids to progression than short tails, mice of all of the forms studied showed marked use of the tail during locomotion along small branches. Use of the tail as a balancing organ was evident whenever balance became difficult, the tail movements serving to counterbalance the continuous shifts in the center of gravity of the body of the moving animal. Here again the greater effectiveness of the longer tail was evident; not only could the tip circumscribe a greater arc without seriously dislodging the hind quarters of the mouse, but a recovery of balance requiring only a slight movement of a long tail required a greater movement of a short tail. Thus, a long tail, as well as being able to do all that a short tail can, is capable of achieving a precision of balance unattainable by the short tail.

In addition to use as a balancing organ, the tail serves as a prehensile organ, a prop, or a tactile organ. The prehensility is apparent whenever a mouse attempts to recover its upright position after its hind feet have slipped from the upper surface of a branch. The tail is flexed over the branch and either helps brace the animal, while it pulls itself upright, or helps pull the mouse into the upright position. If another branch is within reach, the tail may be flexed over that instead, but used similarly. Employment as a prop is sometimes observed during times of precarious progression, when the tail is held tautly against a nearby branch in such a manner as to brace the unsteady body of the mouse against that branch, or during times of leisurely progression, when the tail, together with the hind legs, supports the animal as it raises the forelegs to wash, eat, or investigate. Tactile use is evident whenever the gently waving tail touches a nearby branch and then remains close to it, often even in contact, but not pressed against it. The tail is kept ready to press against or to flex over such a branch, should slipping of the hind feet seem imminent. As a tactile organ the tail informs the brain of the presence of nearby branches which may be used in time of need. As the mouse's progression becomes increasingly arduous, waving of the tail becomes more marked, and accessible branches are thus more likely to be located. Since the several functions of the tail are closely related, it is often difficult to isolate one from another, but instances of each of these four have been observed in which the long tail of the semiarboreal forms was more useful during locomotion along small branches than was the shorter tail of the terrestrial forms.

The foregoing discussion of tail use as related to the progression of peromyscus leads to further consideration of various relationships between body proportions and climbing ability. The tail-amputation experiments have demonstrated a positive correlation between tail length and proficiency in climbing along small artificial branches; and there are undoubtedly several additional relationships between body measurements and climbing proficiency. The rather widespread tendency, for example, of the semiarboreal forms to have hind feet which are both absolutely and relatively longer than those of terrestrial forms may be correlated in some way with climbing ability. Because of the impracticability of obtaining precise measurements of the feet of living mice and because, also, of the difficulty of isolating the foot-length factor in experiments designed to measure the comparative abilities of a relatively large number of forms of peromyscus, no persistent attempt was made to determine such a correlation in the present investigation. Moreover, in studying the relationship of foot size to climbing ability it would be necessary to consider the degree of development of the plantar tubercles, since these tubercles show considerable variation in prominence among the several forms studied. The consideration of foot size with regard to arboreal adaptation is complicated, too, by the fact that foot size may respond to the demands not only of arboreal activity, but of locomotion on loose sand. The latter type of adaptation has been suggested by Hayne (1950: 39, 51, 53) for leucocephalus and closely related coast-dwelling mice, all of which have longer hind feet than do closely related forms living inland on less sandy soil. Such an adaptation would be comparable in function to that so frequently noted in descriptions of Lepus americanus, the relatively large-footed snowshoe hare (Anthony, 1928: 483; Burt, 1946: 242; Cahalane, 1947: 583).

Body weight, as well as tail length, is related to climbing ability. A heavy mouse produces greater swaying of a small, flexible branch than does one of lesser weight. Greater swaying of the branch, in turn, renders the maintenance of balance more difficult. Weight may also affect other aspects of climbing. One obviously obese animal was unable to climb certain roughened vertical tubes, which several days later, after it had assumed a weight comparable to that of its cage-reared relatives, it climbed quite easily. Although mice which showed evidence of obesity were excluded from the experiments, the weight of any mouse nevertheless varied from time to time. Furthermore, since captive peromyscus are usually heavier than newly captured wild specimens, a fact first noted by Sumner (1932: 18), there is some question as to how accurately the weights of laboratory mice represent the weights of the same forms under natural conditions.

Relationship of body weight to climbing ability is extremely complex. In this study the semiarboreal forms were heavier, in general, than the terrestrial ones, greater weight being correlated with greater body size of the particular semiarboreal stocks used (Tables V and VII). Since the semiarboreal forms also exhibited greater climbing ability, in general, than the terrestrial forms, body weight showed a positive correlation with the climbing ability of the several forms. Within the form bairdi, however, was found a significant negative correlation (r equals -.69) between body weight and ability of the mice to climb roughened vertical tubes of progressively greater diameters. It may well be, therefore, that ability in this type of climbing is positively correlated with general body size and that weight, because it is generally dependent on body size, shows a similar positive correlation with the climbing ability in mice of marked differences in body size; whereas a negative correlation of this ability with weight is apparent only when abilities of mice of similar body lengths are compared.

It is evident from the experiments and observations described that the longer-tailed, semiarboreal forms surpassed the shorter-tailed, terrestrial forms in climbing proficiency, but the performance of the Hood River rubidus, of somewhat intermediate status, warrants separate discussion. The rubidus scores for jumping ability and crossing of roughened glass tubes fell within the range attained by the semiarboreal rather than the terrestrial forms (Tables IX and XII). Although each score for rubidus was based on the performance of only one mouse, extraexperimental observations of such performance by rubidus support their general validity. Since the Hood River rubidus aligns with the semiarboreal rather than with the terrestrial forms in relative tail length, these performance scores are in harmony with the general correlation between tail length and arboreal ability. In ability to climb roughened vertical glass tubes (Tables V and VII), however, rubidus was more or less intermediate between the terrestrial and the semiarboreal groups, and its scores were actually closer to those of the terrestrial than to those of the semiarboreal mice. One possible explanation for this apparent discrepancy is that body length, which showed a significant correlation with ability to climb roughened vertical tubes, is of primary importance in this type of performance. The average body length of the rubidus tested was more like that of the terrestrial than that of the semiarboreal forms (Tables V and VII). It may be that the small body size of rubidus, as of the gambeli studied by McCabe and Blanchard (1950), so facilitates its finding of ready refuge in incidental cover as to constitute in itself one of the chief adaptations for survival. McCabe and Blanchard, in discussing the importance of size and its relationship to mode of life, have pointed out that rodents but a little larger than gambeli must resort to such adaptations for survival as climbing or digging. Certainly, the results of this investigation favor such a conclusion to the extent that they show that it is, in general, the larger forms of the genus Peromyscus which demonstrate the better climbing ability. Other differences in body proportions, not yet studied, may offer information relevant to the climbing proficiency of rubidus. Clark (1941: Table 4) calculated that a stock of rubidus from Eugene, Oregon, had a relatively shorter femur, as compared with foot length, than did any of the other nine forms of peromyscus, including 41 different stocks and both terrestrial and semiarboreal forms. Since span appeared to be a very important factor in the climbing of the tubes, possibly rubidus, if the ratios of some or all of the long bones of its legs are smaller than the same ratios in the other forms studied, is somewhat handicapped by virtue of its relatively shorter legs. Whatever the explanation of the climbing ability of the Hood River rubidus is, this stock, although better adapted to arboreal habits than the terrestrial forms tested, is not so well adapted for scansorial performance as the semiarboreal forms studied. It is, moreover, evident that scansorial ability is facilitated by factors other than the mere possession of a long tail.

With regard to general habits, peromyscus may be regarded as terrestrio-arboreal, with some of its forms more arboreal than others. References to the arboreal activity of the semiarboreal forms included in the present study have been cited in an earlier part of this paper. Records of the arboreal behavior of certain other forms of peromyscus are also available. Cahalane (1939: 433) reported that several Peromyscus boyli rowleyi which "escaped while being transferred from traps to cages fled into trees in preference to running on the ground." This habit of taking refuge in trees had earlier been noted by Dice, who observed the progression of rowleyi mice from tree to tree by way of interlacing branches and was able to photograph one in an oak tree into which it had climbed (Dice and Blossom, 1937: 36, Pl. 2). The tree nests of three subspecies of Peromyscus nuttalli have been described by several authors (Pickens, 1927: 246-47; Welter and Sollberger, 1939: 80-81; Lewis, 1940: 427; Barbour, 1942: 90-91; Moore, 1946: 57). There is no doubt, therefore, that scansorial activity plays an important role in the lives of many of the forms of the genus Peromyscus.

Even though they may nest in trees or climb trees in search of food or to escape from predators, the most arboreally inclined of the peromyscan forms are at home on the ground. Results of the present study, together with previously reported experimental work, indicate that in peromyscus semiarborealness is distinguished from terrestrialness in some highly complex manner. Clark (1936) found that three semiarboreal and three terrestrial forms differed in geotropic behavior. Mice of the semiarboreal group studied by him were more sensitive to slight inclinations and responded by traveling along higher orientation angles to slopes than did mice of the terrestrial group. More recently Harris (1952), working with the semiarboreal gracilis and the terrestrial bairdi, demonstrated that each of these tends to select an artificial habitat which simulates its natural one. In the present study a diversified group of peromyscan forms showed a correlation in tail length, climbing ability, and reaction to elevation with natural habit. Additional information offered by this and the two studies cited above makes clear that the terrestrial forms all exhibited to at least some degree whatever feature is of particular adaptive value to the forms of scansorial habits. The semiarboreal forms, it is true, are better adapted for scansorial existence than are the terrestrial ones, but there remains the question of why the forms classed as terrestrial do virtually no climbing under natural undisturbed conditions, as seems to be the case. All terrestrial peromyscus live in places characterized by some form of climbable vegetation, sparse though it may be. All of the forms studied here were perfectly able to climb and showed no marked aversion to climbing under laboratory conditions. Certainly, the complex of factors influencing the climbing behavior of peromyscus is still little understood, and much additional study is required before the subtleties of the relationship between habit and habitat can be fully explained.

In comparing the climbing ability of peromyscus with that of other mammals, it is evident that even the most arboreal peromyscus are less arboreal than are such forms as, for example, the sloth, the gibbon, and the tree squirrels. The tree squirrels, such as Glaucomys, Tamiasciurus, and Sciurus, represent a category which includes those animals which travel along the upper surfaces of branches by means of all four limbs. To this group, that contains the majority of arboreally inclined mammals, belongs peromyscus, which has evolved according to the general pattern of arboreal adaptation rather than according to the unique pattern of either the sloth or the gibbon.

Among the mammals with adaptations for arboreal locomotion are many forms besides peromyscus in which the tail plays an important role in progression, and in several closely related forms tail length varies directly with arborealness. Although the native microtines are, in general, terrestrial, fossorial, or semiaquatic, there are two species of Phenacomys, longicaudus and silvicola, which, because of their largely arboreal habits are known as tree mice. In each of these two species the average tail length is both absolutely and relatively greater than is that of any of the other four species recognized (measurements from Howell, 1926). In the genus Sciurus, the gray squirrel (S. carolinensis), which is a more agile climber than is the fox squirrel (S. niger rufiventer), has a relatively longer tail (see measurements given by Burt 1946). A similar condition exists among murine rats; Rattus rattus is a more skillful climber and has a relatively longer tail than R. norvegicus (see measurements given by Anthony, 1928, and Cahalane, 1947). Likewise, the fisher (Martes pennanti), which is so swift in its arboreal progression as to be able to overtake the marten (M. americana), has a relatively longer tail (see Burt, 1946, and Cahalane, 1947). Although exceptions may occur, the correlation between relative tail length and the climbing proficiency of closely related mammals which run along branches seems to be of fairly universal occurrence.

Not all long-tailed mammals are arboreal, however, nor are all arboreal mammals long-tailed. In the kangaroo rat (Dipodomys) and the jumping mouse (Zapus), the remarkably long tail serves as an equilibrator in adaptation to the leaping habits (Hatt, 1932; Howell, 1932); and the fairly long, laterally compressed tail of the muskrat (Ondatra), on the other hand, acts as a rudder (Cahalane, 1947: 525). Among the several short-tailed mammals which are at home in the trees may be mentioned the sloth (Choloepus and Bradypus) and the gibbon (Hylobates). The balancing function of a tail would be of little use to an upside-down traveler such as the sloth, and special adaptation for long periods of suspension from the branches is gained by marked modifications of the appendages (Britton, 1941) rather than by the development of a long prehensile tail like that of the opossum and certain of the monkeys. The virtually tailless gibbons are primarily brachiators, swinging by their long arms from branch to branch with ease and speed. Where the maintenance of balance is required, as is the case when these animals walk or run along branches, the tremendously elongated arms are held high or extended to the sides and very obviously used as balancing organs (Carpenter, 1940), thus having a function comparable to that of the long tails of certain mammals which use all four of their appendages in running along branches. These are but a few illustrations which indicate not only that a long tail may serve functions other than those concerned with arboreal locomotion, but that arboreal habits are not necessarily dependent upon the development of a long tail.

The differences distinguishing the higher taxonomic categories are generally held to be the result of adaptation. There has been some question, however, as to the adaptive value of the ones used as criteria to distinguish the lower categories. Especially has considerable doubt been expressed from time to time regarding the adaptive value of subspecific differences. That subspecific characters in peromyscus are inherited was first proved by Sumner (1932: 28-30), and it has been confirmed by many later studies. The adaptive value of one of these subspecific characters, that of pelage color, was brought out by the experiments of Dice (1947). The results of the present study demonstrate the adaptive value of another subspecific character, that of tail length. In the wide-ranging genus Peromyscus, therefore, the characters used to differentiate subspecies are not only inherited but, at least in these two instances, are also adaptive.

SUMMARY

A laboratory investigation was made of the climbing behavior and ability of mice of ten forms of the genus Peromyscus. Six of the forms are subspecies of the species maniculatus. Peromyscus maniculatus gracilis, P.m. oreas, P. leucopus noveboracensis, P. nasutus nasutus, and P. truei truei are semiarboreal in their natural habitats; P.m. bairdi, P.m. blandus, P.m. nebrascensis, and P. polionotus leucocephalus live in grasslands or in beach or desert country where trees are relatively infrequent. The stock of P.m. rubidus originated near Hood River, Oregon, at the edge of the coastal forest. The semiarboreal forms differ from the terrestrial forms, in general, in that the tails and hind feet are both absolutely and relatively longer as compared with body length.

Mice of all of the forms climbed to elevated levels when the experimental apparatus offered was sufficiently easy to climb and when the animals were allowed time to explore freely.

In reaction to high places, the semiarboreal forms showed a significantly greater tendency than did those of the terrestrial forms to remain on an elevated platform in the absence of a pathway to the ground. Whether on elevated branches or platforms the semiarboreal mice were also less nervous and more aware of the general relationship to the ground than were the terrestrial.

In vertical climbing, natural tree trunks of moderate roughness were easily climbed by mice of all of the forms, but members of the terrestrial forms exhibited significantly greater difficulty in climbing a trunk of relatively smooth-, hard-barked surface, such as that of the beech (Fagus), than did those of the semiarboreal. Each of the five semiarboreal forms differed significantly from each of the four terrestrial forms in greater ability to climb artificial trunks of several different diameters and grades of smoothness.

In crossing gaps, mice of the semiarboreal forms were able to reach and to jump greater distances than were those of the terrestrial forms. Spontaneous jumping from branch to branch, however, was infrequent.

In climbing horizontally along tubes, roughened and otherwise simulating small branches, the semiarboreal forms exhibited greater proficiency, in general, than the terrestrial. With the single exception of nasutus, each of the semiarboreal forms showed a significantly greater ability, as measured by mean number of performance errors, in traveling along such branches than did any of the terrestrial forms.

Amputation of the tail seriously handicapped the arboreal proficiency of the mice, but the resultant handicap was greater for the long-tailed than for the short-tailed forms. The long tail of the semiarboreal forms of the genus Peromyscus is thus demonstrated to be an adaptive structure which facilitates an existence in semiarboreal habitats. A marked advantage shown by the long tail over the short tail is its greater effectiveness as a balancing organ. The long tail is also more effective than the short tail in prehension, as a tactile organ, and as a prop.

The semiarboreal forms are, as a whole, better adapted for climbing than the terrestrial forms, not only by virtue of their relatively longer

tails, but also because they show less nervousness on elevated branches and greater awareness of the general relationship of their elevated supports to the ground. The climbing performance of rubidus, the stock from a type of habitat intermediate between forest and open field, sometimes was aligned with the performance of the semiarboreal forms and sometimes fell between that of the semiarboreal and that of the terrestrial groups. In mice of the genus Peromyscus, therefore, the results of these experiments bear out that adaptation for arboreal life involves modification of both body proportions and behavior.

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Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $1.25.

PLATE I

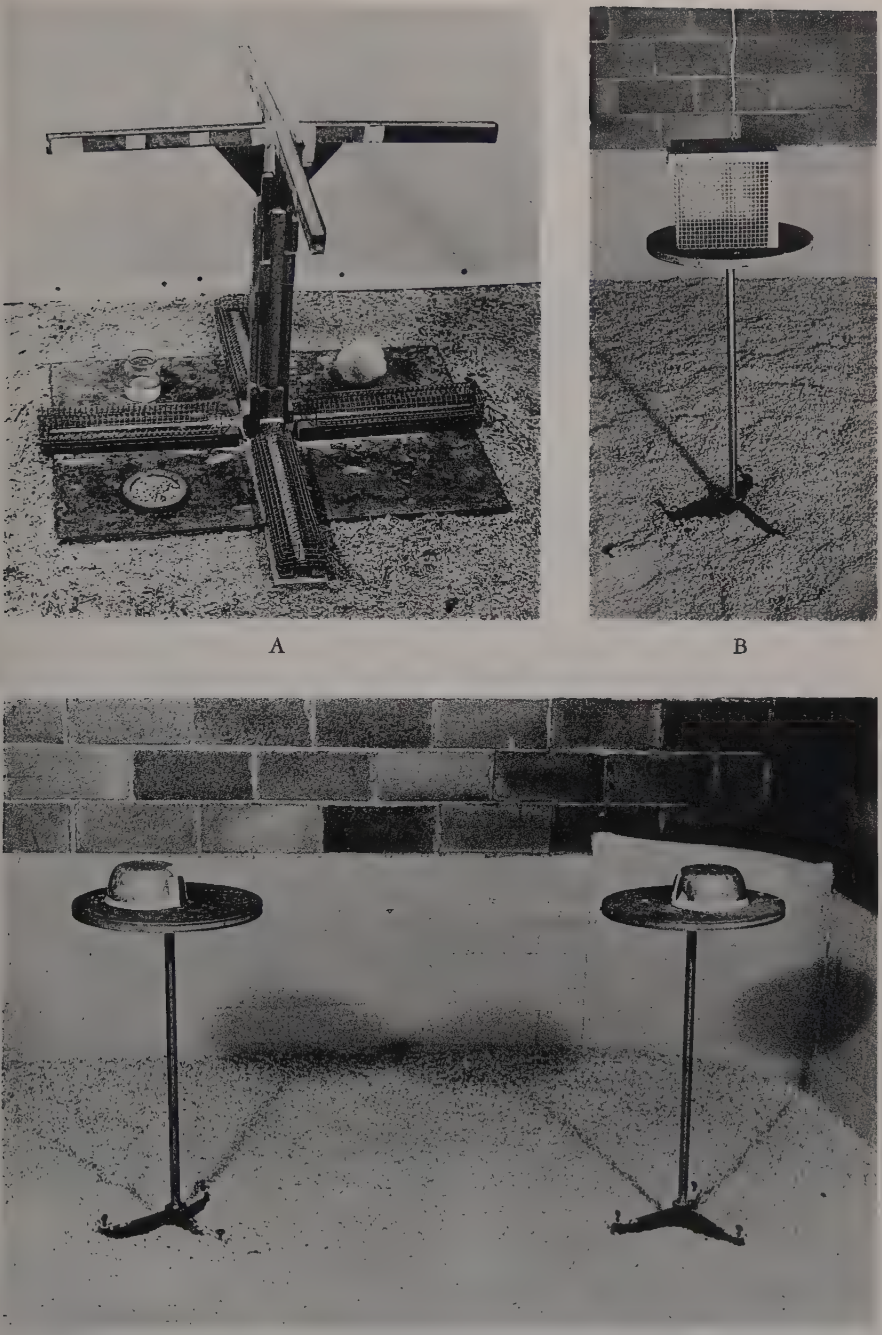
Equipment

Fig. A. Apparatus for study of the reaction of peromyscus to the climbing of easily climbed objects.

Fig. B. Platform and cage used in study of the reaction of mice to elevation.

Fig. C. Apparatus employed in measuring the tube-crossing proficiency of the mice.

PLATE I



A

B

C

PLATE II

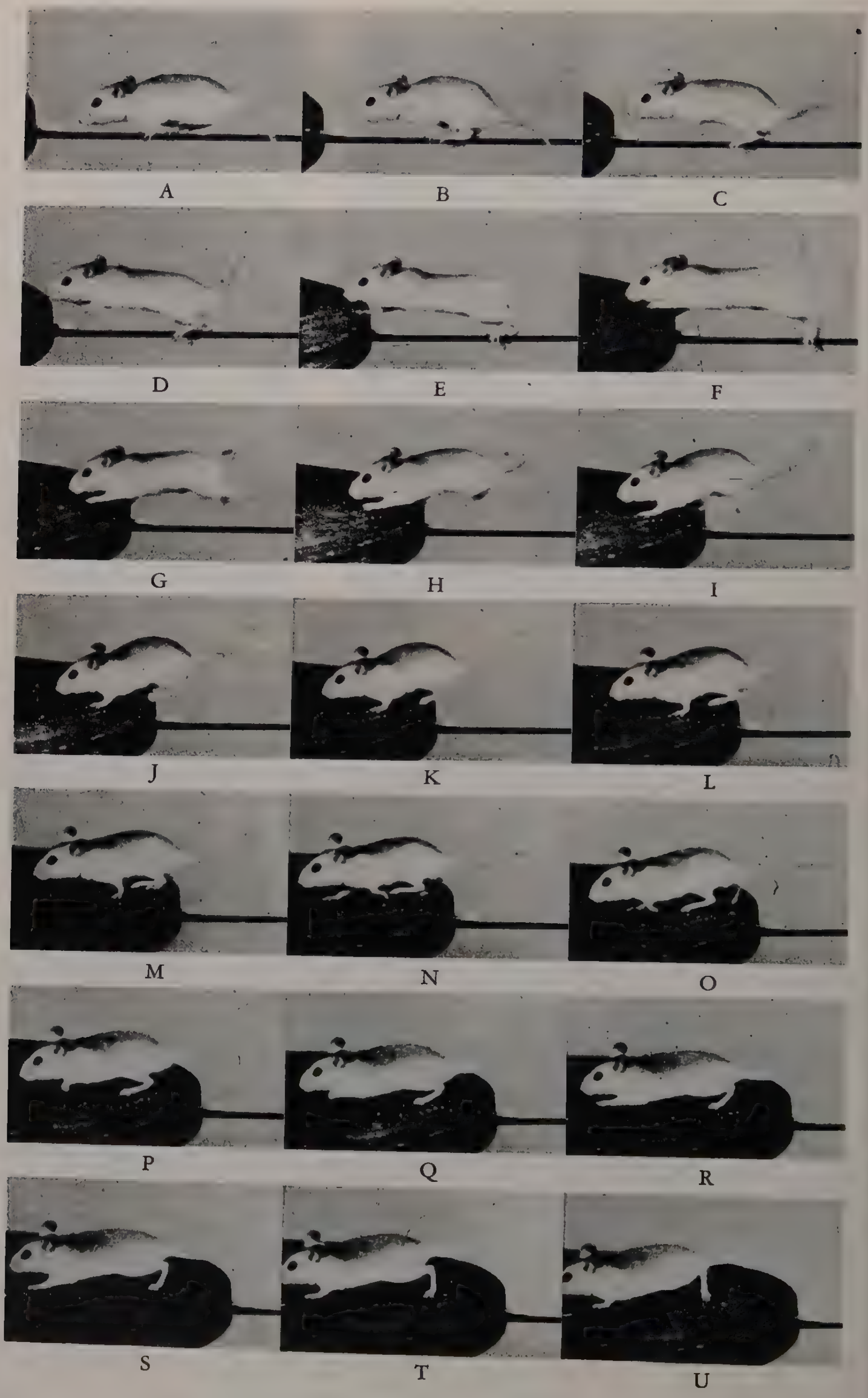


PLATE II

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-U. Peromyscus polionotus leucocephalus bounding from a tube of 3 mm. in diameter onto a platform and walking across the platform. The fore feet left the tube almost simultaneously as later did the hind feet. For a fraction of a second the body of the mouse was unsupported (G, and possibly H). In landing on the platform, the mouse placed its feet in the following order: right fore, left fore, right hind, and left hind, the left hind foot retaining contact with the platform only momentarily. In walking forward on the platform, the mouse placed its feet individually in a characteristic walking order: right fore, left hind, left fore, and right hind. (21 consecutive frames.)

PLATE III

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-D. Peromyscus maniculatus blandus ascending a sloping branch (Lonicera). The tail was raised and moved rapidly as balance became difficult and was flexed under the branch as the mouse began to slip. (Interrupted sequence of frames.)

Figs. E-L. Same blandus mouse descending from one branch to another. The relatively short tail left the upper branch shortly after release of the hind feet and the mouse slipped in landing on the lower branch. Immediately after recovery from slipping the tail was used to maintain balance. (Interrupted sequence of frames.)

Figs. M-P. Peromyscus nasutus nasutus descending a tree trunk (Acer negundo). The tail was held close to but not pressed against the trunk. The feet were placed individually and the degree of rotation of the hind limbs was less than that frequently observed in tree squirrels. (Interrupted sequence of frames.)

Figs. Q-T. Same nasutus ascending the same tree trunk. The tail was held close to the trunk but not pressed against it. The feet were moved individually. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus polionotus leucocephalus ascending the same Acer negundo trunk. The locomotion of the mouse, which moved the hind legs together, illustrates a mode of ascent occasionally employed by peromyscus, but far more frequently by the tree squirrels. (4 consecutive frames.)

PLATE III

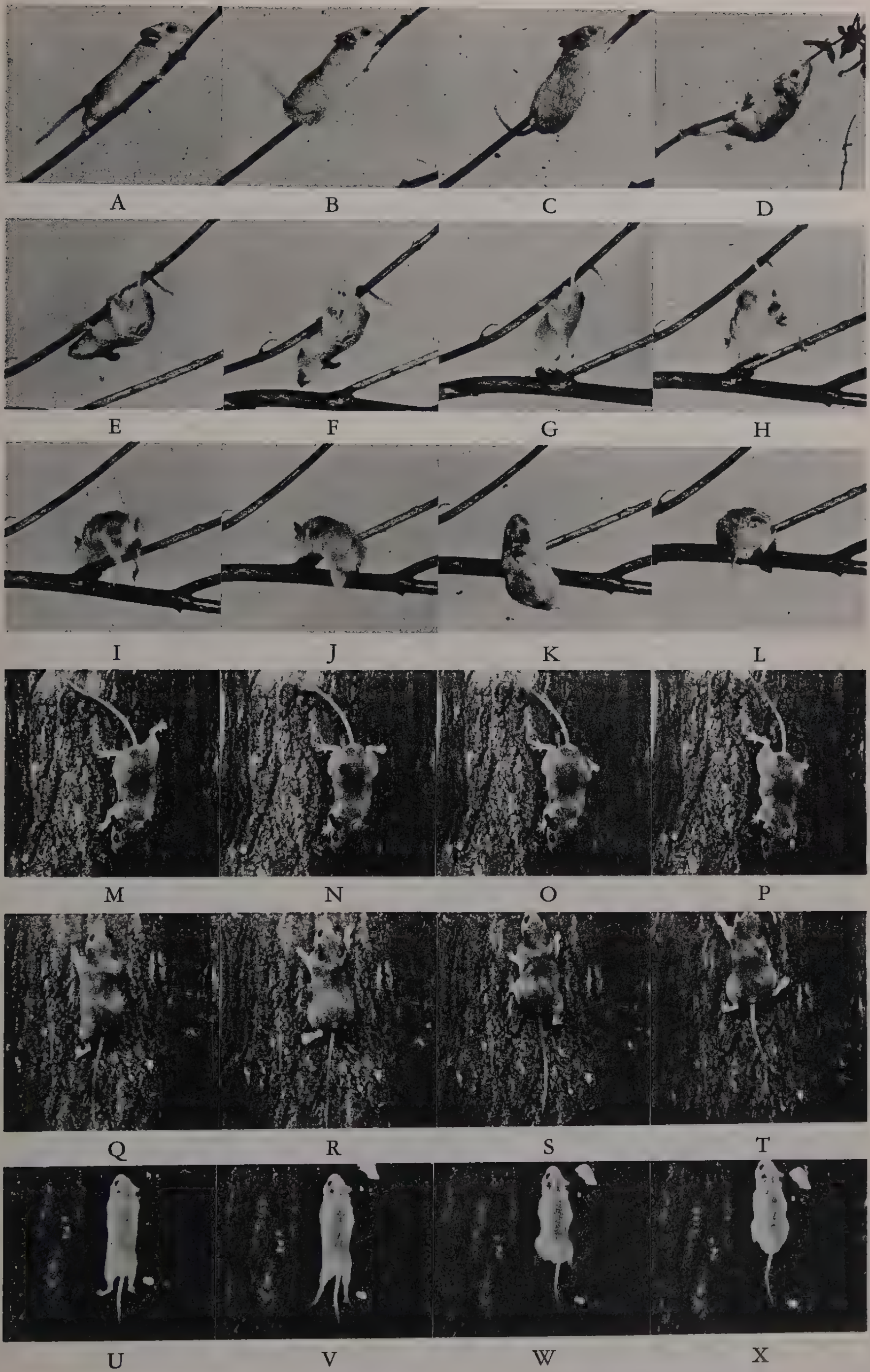


PLATE IV

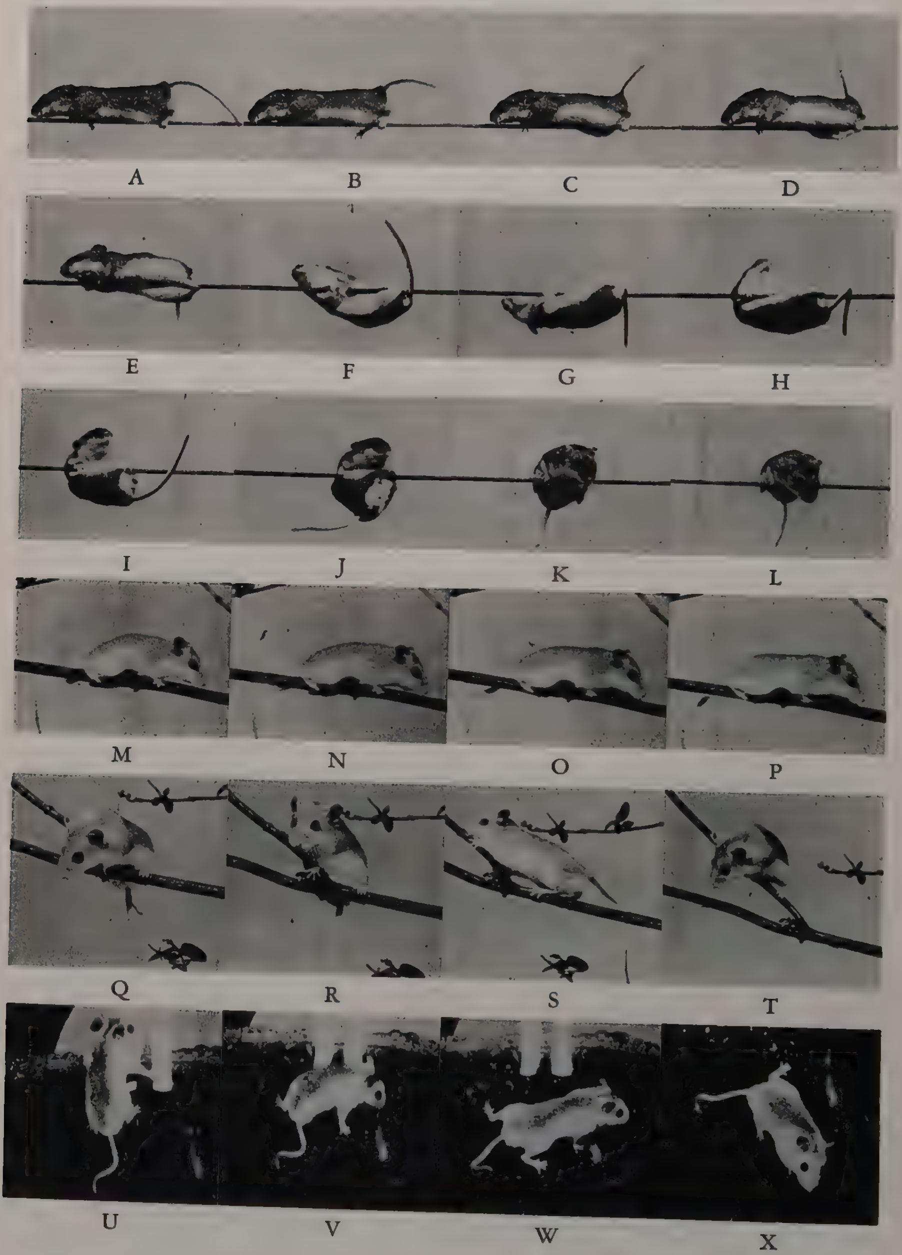


PLATE IV

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-D. Peromyscus maniculatus bairdi crossing a roughened tube of 3 mm. in diameter. Slipping of the right hind foot from the tube was not followed by slipping of the body below the tube. Balancing movements of the tail were evident. (4 consecutive frames.)

Figs. E-L. Same bairdi mouse slipping below the tube. Note use of the feet and tail in recovery of mouse from inverted position. (Interrupted sequence of frames.)

Figs. M-P. Peromyscus maniculatus nebrascensis flexing the proximal part of its tail under a branch and then gradually releasing its tail hold on the branch as loss of balance becomes less imminent. (4 consecutive frames.)

Figs. Q-T. Same nebrascensis mouse showing the placement of its toes. The spreading of the toes of the left fore foot is evident (Q, R, and S). In S the hind toes are also widely separated. In Q, R, and T, where the mouse is sitting crosswise on the branch, the toes of the visible hind foot are held closer together. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus polionotus leucocephalus using its tail as a prop (U and V), as a combined prop and prehensile organ (W), and as a prehensile organ only (X). The mouse was turning about near the top of a section of tree trunk (Acer negundo). The tail was braced against a projecting piece of bark as the front feet of the mouse encountered and then turned away from a smooth-surfaced obstacle at the top of the trunk. In turning downward the mouse used its tail progressively less as a prop and progressively more as a prehensile organ. (Interrupted sequence of frames.)

PLATE V

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-F. Peromyscus leucopus noveboracensis making a successful descent from one to another of two somewhat flexible branches (Lonicera). The tail in maintaining its hold on the upper branch all the while that the hind feet were being lowered to the other branch, retarded the rate of falling of the hind quarters of the mouse and thereby facilitated accurate placement of the hind feet on the lower branch. (Interrupted sequence of frames.)

Figs. G-R. Same noveboracensis mouse, having attempted to reach down to the branch leading to the igloo, reaches down to the shorter branch in the foreground. This branch, together with the longer branch, was then pulled closer to the upper branch by the mouse. The animal next reached over to the longer branch, onto which it lowered the rest of its body. The tail was used to retard the rate of falling of the hind quarters. The flexibility of the branches, particularly of the lower ones, is apparent from their very noticeable bending under the weight of the mouse. (Interrupted sequence of frames.)

PLATE V

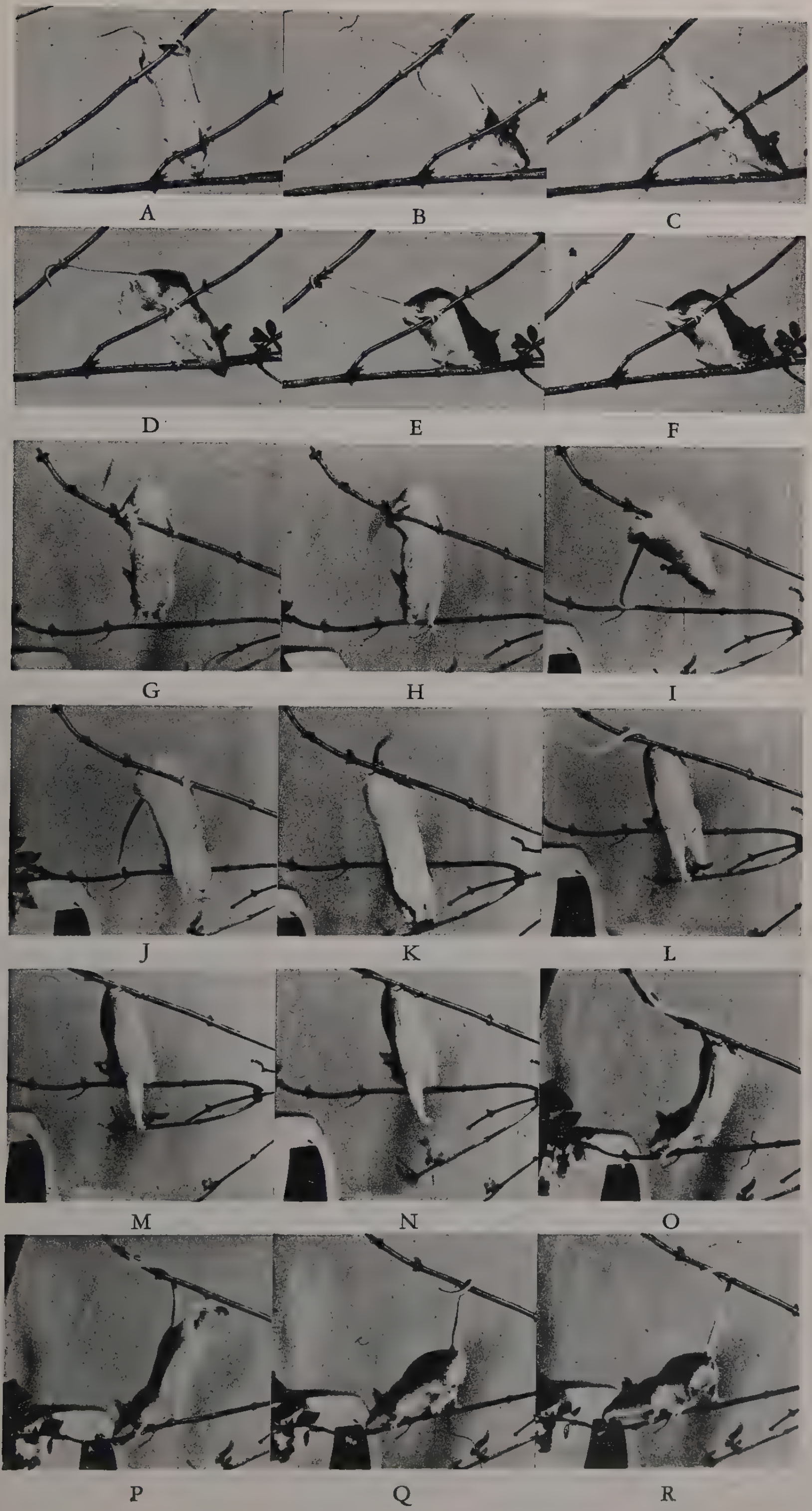
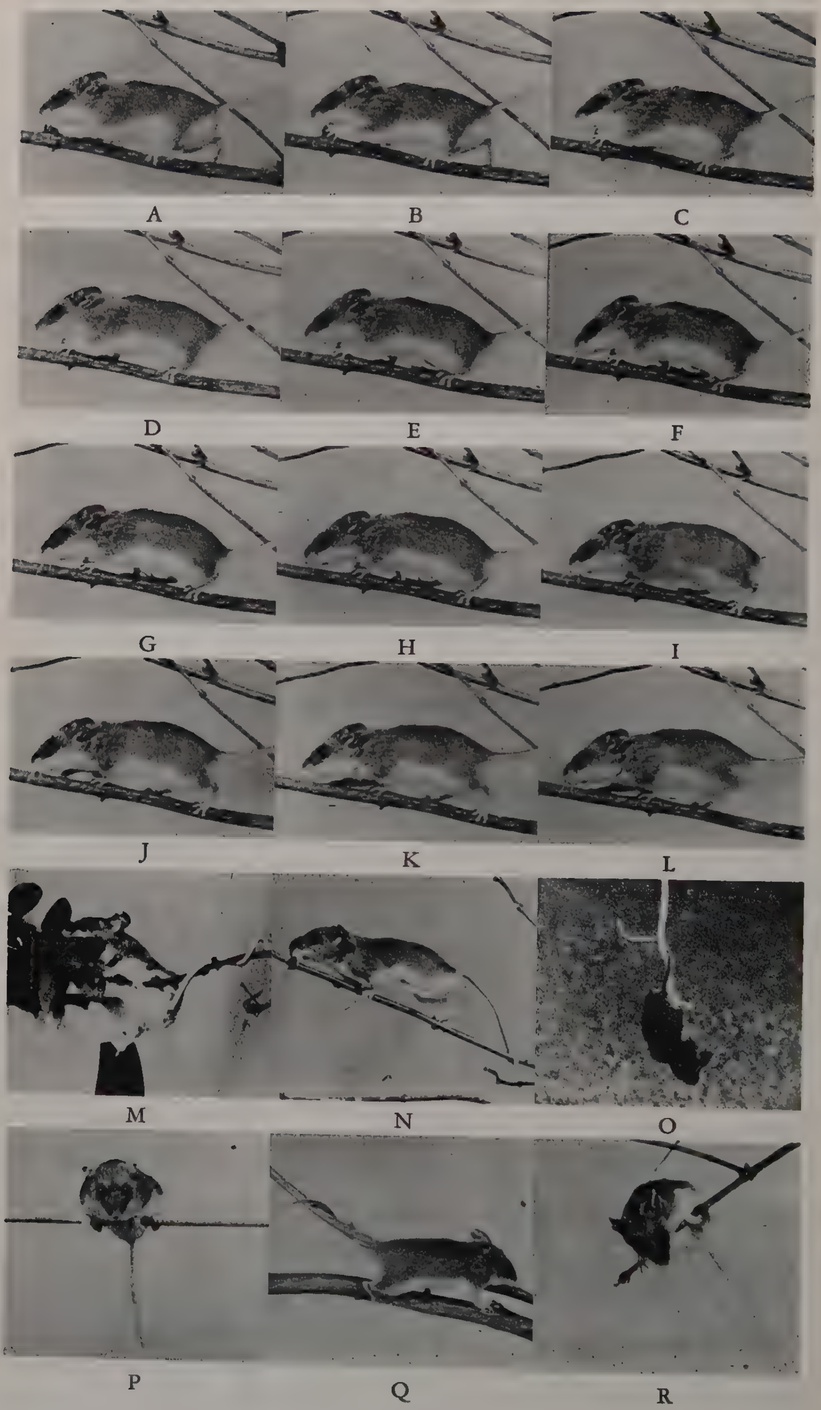


PLATE VI



A B C

D E F

G H I

J K L

M N O

P Q R

PLATE VI

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-L. Peromyscus maniculatus gracilis traveling along a branch. Note the spreading of the toes of both the fore and hind feet. The order in which the feet were raised is as follows: left fore, right hind, right fore, and left hind. (12 consecutive frames.)

Fig. M. Peromyscus leucopus noveboracensis using its prehensile tail in recovering its upright position on a flexible branch.

Fig. N. Same noveboracensis mouse progressing along a branch with the tip of its tail flexed loosely below that branch.

Fig. O. Peromyscus maniculatus gracilis flexing its tail around a cord in such a manner as to decrease the rate of descent.

Fig. P. Peromyscus maniculatus bairdi sitting crosswise on a tube 3 mm. in diameter. The toes of the hind feet grasped the tube and the fore legs rested on the tube. The fore feet were not in contact with the support.

Fig. Q. Peromyscus maniculatus gracilis showing prehensile use of the tail as the animal progressed from one to another of two nearby branches.

Fig. R. Same gracilis mouse sitting crosswise near the end of a flexible branch in a position similar to that of bairdi (Fig. P). The tails of both of these mice are straight and taut and are of great importance in the maintenance of these sitting positions.

PLATE VII

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-L. Peromyscus maniculatus gracilis spanning a gap of 10.5 cm. in reaching downward from one tube to another. The tail was flexed over the upper tube both before and after the hind feet were released. The front feet were placed almost simultaneously on the lower tube as later were the hind feet. (Nonconsecutive frames for the most part.)

Figs. M-T. A tailless gracilis mouse spanning a gap of approximately 5 cm. in reaching downward. The feet were placed individually on the lower tube, the two hind feet following the two fore feet. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus truei truei using its tail as a balancing organ (U and V) and then flexing it over (X) a branch which has been touched (W).

PLATE VII